Landscape characteristics and honeybee colony integrity: A case study of Mwingi, eastern Kenya

by

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SUMMARY

Honeybees (*Apis mellifera*) are highly efficient crop pollinators, providing valuable ecosystem services through pollination in diverse environments globally. However, honeybee populations are in decline and habitat loss and fragmentation, pests and parasites and nutritional deficiencies are emerging as some of the most important factors contributing to this decline, consequently threatening food security and rural communities' livelihoods. Therefore, monitoring the interconnected effects of landscape fragmentation, pollen diversity, honeybee pests' and honeybees' colony strength is a fundamental component of their conservation as well as safeguarding continued ecosystem services. In Kenya, where the study is carried , there have been no investigations specifically addressing these linkages mainly because until recently, there has been unavailability of freely available moderate to high resolution landscape fragmentation maps. As such, the overall goal of this study was to quantify landscape fragmentation, and to investigate its effect on honeybee colony strength, pollen diversity and protein content and *Varroa destructor* mite occurrence in a semi-arid region located in the eastern part of Kenya.

Using Sentinel-1A SAR and Sentinel-2A optical remote sensing systems, the first part of this study examined the use of a random forest machine learning algorithm to map fine-scaled and under-represented landscape elements representing honeybee habitats in six study sites (apiaries) specifically selected based on varying landscape degradation levels. The results indicated that the fused SAR and optical imagery had the highest overall accuracy for mapping the spatially explicit honeybee habitats and thereafter, fragmentation metrics relating to landscape composition and configuration were derived from this fused combination, within a 3 km buffer radius of each apiary.

Landscape fragmentation metrics derived from the fused SAR and optical imageries were thereafter linked with honeybee colony strength parameters. Results of zero inflated negative binomial regression with mixed effects indicated that lower complexity of patch geometries represented by Fractal Dimension and reduced proportions of croplands were most influential at local foraging scales (1 km) from the apiary, while higher proportions of woody vegetation and hedges resulted in higher colony strength at longer distances from the apiary (2.5 km). Moreover, honeybees in moderately degraded landscapes displayed the most consistently strong colonies throughout the study period.

In the third part of the study, pollen diversity and protein content were examined across the six apiaries. Results showed that pollen diversity was highest in moderately degraded landscapes while protein content in pollen did not vary by location but varied by seasonality. In the final part of the

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study, *Varroa destructor* mite did not have any effect on honeybee colony strength parameters, except for eggs. However, lower complexity of patch shapes and greater landscape homogeneity represented by the Shannon diversity index were highly influential on *Varroa destructor* mite occurrence.

The overall study shows that landscape fragmentation influences honeybee colony strength, pollen diversity and *Varroa destructor* mite occurrence. These results can be used to inform hive placement for maximal colony strength and hive productivity. However, the study was conducted in only six apiaries and recommendations regarding validation at larger numbers of replicates are made.

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Opsomming

Die heuningby (*Apis mellifera*) is ‘n hoogs doeltrefende bestuiwer van gewasse en verskaf waardevolle ekosisteemdienste deur bestuiwing wêreld-wyd in diverse omgewings. Egter, heuningby populasies is aan die afneem as gevolg van fragmentasie, peste en siektes, en voedings tekorte, as sommige van die belangrikste faktore. As voortvloeisel hiervan word voedsel-sekuriteit en die lewensbestaan van plattelandse gemeenskappe bedreig. Daarom is die monitering van die tussen-verbintenis van landskapfragmentasie, stuifmeeldiversiteit, heuningbypeste en heuningbykoloniesterkte ‘n fundamentele komponent van hul bewaring en voorgesette ekositeemdienste. In Kenja, waar hierdie studie uitgevoer is, was daar nog nooit enige ondersoeke wat spesifiek hierdie verbintenisse aanspreek nie. Dit is hoofsaaklik as gevolg van die tot onlangse onbeskikbaarheid van vrylik bekombare, hoë-resolusie landskapfragementasiekaarte. Sodoende was die oorhoofse doel van hierdie studie om lanskapfragmentasie en om die uitwerking hiervan op heuningbykoloniesterkte, stuifmeeldiversiteit en proteïn-inhoud, en die voorkoms van die *Varroa destructor* myt, in ‘n semi-dorre streek in die Oostelike deel van Kenja te kwantifiseer.

Met behulp van Sentinel-1A SAR en Sentinel-2A optiese afstandswaarnemingstelsels, het die eerste deel van hierdie studie 'n ewekansige ‘forest’-masjienleer algoritme gebruik om die fynskaalse en onderverteenwoordigde landskapselemente wat heuningbyhabitatte voor te stel in ses studiepersele (byekorf-staanplekke of ‘apiaries’), spesifiek gekies op grond van hul verskillende landskap-agteruitgangsvlakke. Die resultate het aangedui dat die versmelte SAR en optiese beelde die hoogste algehele akkuraatheid het vir die kartering van die ruimtelike eksplisiete heuningbyehabitatte. Hierna is fragmenteringsmetrieke afgelei van hierdie versmelte kombinasie, met betrekking tot landskapsamestelling en -konfigurasie binne 'n buffer-radius van 3 km van elke byekorf-staanplek.

Landskapsfragmenteringsmetrieke afgelei van die versmelte SAR en optiese beelde is daarna gekoppel aan heuningbysterkte-parameters. Resultate van nul-opgeblase negatiewe binomiale regressie met gemengde effekte, het aangedui dat laer kompleksiteit van kol-geometrieë wat deur Fraktaledimensie voorgestel word, en die verminderde proporsies van gewaslande, die invloedrykste was op plaaslike voedingsbronne vanaf die byekorwe (1 km), terwyl hoër verhoudings in houtagtige plantegroei en heinings in hoër koloniesterkte op langer afstande vanaf die byekorwe (2,5 km) tot gevolg gehad het. Boonop het heuningbye in matig-agteruitgaande-landskappe die mees bestendigste sterk kolonies gedurende die studietydperk gehaad.

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In die derde deel van die studie is stuifmeeldiversiteit en proteïeninhoud oor die ses byestaanplekke ondersoek. Resultate het getoon dat stuifmeelverskeidenheid die hoogste was in matig-agteruitgaande-landskappe, terwyl die proteïeninhoud in stuifmeel nie volgens plek varieër het nie, maar wel volgens seisoenaliteit. In die laaste gedeelte van die studie het *Varroa destructor* myt geen effek gehad op die sterkteparameters van heuningbykolonies nie, behalwe vir eier telings. Laer kompleksiteit van kolvorms en groter landskaphomogeniteit wat deur die Shannon-diversiteitsindeks voorgestel word, het egter 'n groot invloed gehad op die voorkoms van die *Varroa destructor* myt.

As ‘n geheel dui die studie dat die fragmentering van die landskap die sterkte van die heuningbykolonie, die stuifmeelverskeidenheid en die voorkoms van *Varroa destructor* myt beïnvloed. Hierdie resultate kan gebruik word om korfplasing in te lig vir maksimale koloniesterkte en korfproduktiwiteit. Die studie is egter in slegs ses byekorf-staanplekke uitgevoer en aanbevelings oor validering met groter getalle herhalings word gemaak.

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This dissertation is dedicated to my family. You are truly God-sent, and you enhance my life with your presence, love, and laughter.

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Biographical sketch

Pamela Aor Ochungo has a background in geoinformation sciences and its application to research and development projects in developing countries' environmental and agricultural systems. She attained her Bachelor of Science in Surveying (BSc Surveying) at the University of Nairobi, Kenya, and a Master of Science in Geoinformation Science (MSc Geoinformation Science) at the Manchester Metropolitan University, UK. She obtained a PhD scholarship from the Deutscher Akademischer Austauschdienst (DAAD) under the African Regional postgraduate Programme in Insect Science (ARPPIS) scholarship programme at the International Centre of Insect Physiology and Ecology *(icipe)* in Nairobi within the Bee Health Programme. The specific aim of her current research is to assess the effects of landscape fragmentation on honeybee colony strength, pollen diversity and its protein content, *Varroa destructor* occurrence, as well as the effects of *Varroa destructor* on honeybees colony strength in eastern Kenya.

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To God my Father in heaven, who has made all things possible; I owe it all to you!

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Preface

This dissertation is presented as a compilation of six chapters. Each chapter is introduced separately and is written according to the style of the journal *Geocarto International* to which Chapter Two was submitted for publication.

Chapter 1	General Introduction and project aims
Chapter 2	Multi-sensor mapping of honeybee habitats and their fragmentation in agroecological landscapes in Kenya
Chapter 3	Fragmented landscapes affect honeybee colony strength at diverse spatial scales in agroecological landscapes in Kenya
Chapter 4	Pollen diversity and nutritional content in differentially degraded semi-arid landscapes in Kenya
Chapter 5	Does the presence of *Varroa destructor* influence honeybee colony strength in fragmented landscapes?
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1 CHAPTER ONE: GENERAL INTRODUCTION

Semi-arid landscape in Mwingi sub-county (Photo credits: Pamela Ochungo, 2017)

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1.1 Background

Honeybees (*Apis mellifera*) through pollination provide valuable ecosystem services via pollination in various habitats, contributing great economic value to crop production globally (Hung et al., 2018; Potts et al., 2010). Furthermore, honeybees are highly beneficial insects well known for their direct supplementation of human diets by means of honey production (Potts et al., 2010). The honeybee is widely distributed globally with the exception of some oceanic islands and the Antarctica (Hung et al., 2018). Due to their high numbers and ease of management, the honeybee appears to be the most prolific of crop pollinators (Delaplane & Mayer, 2000; Watanabe, 1994; Genersch, 2010). Additionally, there is evidence that honeybees are capable of boosting yields in 96% of crops pollinated by animals (Cane et al., 2007).

However, honeybee populations are in decline and a significant amount of scientific research is being undertaken in order to understand the reasons for this decline (Becher et al., 2013; Potts et al., 2010b; Smith et al., 2013). While findings concerning these declines have been mixed, there is a general consensus that several factors, including habitat loss and fragmentation, parasites and diseases, pesticides and agrochemicals, nutritional deficiencies and climate change, are largely contributing to the observed trend (Goulson et al., 2015). Moreover, the modification of flower-rich natural and semi-natural environments to agricultural lands has been a dominant contributor of persistent declines in bees mainly due to reduction in floral resources (Goulson et al., 2015).

A crucial component of honeybee ecology that is beginning to emerge from several studies is the entangled association between honeybee colonies and their landscape. Honeybees require considerable amounts of nectar and pollen for which they can travel great distances to satisfy (Seeley, 1995). This therefore implies that strong honeybee colonies rely greatly on not only their proximal environment but on the wider landscape within its foraging range (Sponsler, 2016). Nonetheless, land use changes occasioned by agricultural intensification and settlement threaten honeybee populations by disrupting forage availability within the landscape and thus affecting the wellbeing of colonies (Ricketts et al., 2008). Moreover, landscape fragmentation resulting from changes in land use have been shown to be one of the key threats to pollination services (Kremen et al., 2002; Steffan-Dewenter & Westphal, 2008). Additionally, pollen diversity has been unequivocally connected with landscape composition and configuration (Matthias et al., 2015) and has been shown to improve honeybee colonies strength as it is an essential component for their wellbeing (Rasmont et al., 2005; Somerville & Nicol, 2006). This is mainly due to the pollen protein content, which is a necessary nutrient especially for brood development (Degrandi-hoffman et al., 2010; Alaux et al., 2017; Keller et al., 2005). A case in point is that whereby pollen harvested from landscapes consisting largely of

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intensive farmlands demonstrated lower nutritional value than those from landscapes with considerable flowering (Requier et al., 2015; Dolezal et al., 2016; Donkersley et al., 2014). Thus, the close and complex relationship between the landscape and honeybee colonies cannot be over emphasized. Furthermore, not only are honeybee colonies directly affected by landscape structure and pollen diversity, but also by the occurrence of pests and parasites in their environment. A well-known honeybee pest, the *Varroa destructor* (Parasitiformes; Varroidae), forms part of a multiple structure of stressors that affect honeybee health in various ways (Locke et al., 2012; Rosenkranz et al., 2010; Evans & Cook, 2018) and has globally been classified as the most critical pest in apiculture (Yves et al, 2010; Francis et al., 2013). Therefore, monitoring the intertwined effects of landscape structure with honeybees' colony strength remains a crucial component of their conservation and thus further downstream, ensuring continued ecosystem services as well as food security due to sustained pollination.

It is nonetheless crucial to distinguish between habitat fragmentation and loss, particularly given that the two terminologies are frequently used interchangeably (Fahrig, 2017; Didham et al., 2012). Habitat fragmentation has been described as the process by which the landscape is split into smaller patches of lower area, resulting in greater isolation of the patches by habitats which are disparate (Fahrig et al., 2019; Fischer & Lindenmayer, 2006). On the other hand, habitat loss has been defined as a process whereby destruction of the habitat occurs over a period of time, mainly as a result of anthropogenic activities (Fahrig, 2017). However, it is contended that habitat fragmentation and loss are highly interlinked and it is difficult to disentangle one from the other (Fletcher et al., 2018). Habitat loss has emerged as a key factor in the decline of bees (Foley et al., 2005) due to a reduction in the available forage resources for the bees while habitat fragmentation affects honeybee populations due to the inability of the small patches to support viable bee populations or owing to isolation which results in inbreeding and consequently weaker bee populations (Brown & Paxton, 2009).

Up to now, the relationship between landscape fragmentation and honeybee colony strength has not been well explored in Africa, unlike in European and North American countries (Aizen & Feinsinger, 1994 ; Brosi et al., 2008). This is particularly worrisome especially since landscape degradation and fragmentation are swiftly increasing in the continent due to rapid human population growth (Cohen, 2003). Accurate mapping of potential honeybee habitats and their fragmentation levels, as well as robust methods for estimation of honeybee colony strength parameters provide valuable information for beekeepers, agricultural extension officers and policy makers as to the suitability of the landscape

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for beekeeping activities. Recent developments in freely available, yet moderate-to- high resolution space-based remote sensing technologies have presented unparalleled opportunities for the quantification of fine-scaled honeybee habitats (European Space Association [ESA], 2017). These high-resolution mapped honeybee habitats can subsequently be associated with honeybee colony strength parameters for improved landscape-scale assessments of habitat suitability for honeybees. Therefore, this study aimed at addressing the interesting research question and fill the current knowledge gap. The study aimed at addressing the linkages between honeybee colony strength, pollen diversity and preferences of honeybees, hive productivity and specific spatially explicit changes in landscape structural patterns (i.e. human induced land cover change, habitat fragmentation and structure). This dissertation is contextualized in the Eastern province of Kenya, an area which is a traditional beekeeping region, and facing several challenges regarding sustainability of beekeeping, which is a major livelihood pathway for the people therein.

1.2 Landscape fragmentation and honeybee colonies in agroecological landscapes in Kenya

Landscape fragmentation and habitat loss has been demonstrated to have one of the greatest negative impacts on honeybee colonies worldwide (Kremen et al., 2002; Steffan-Dewenter & Westphal, 2008). Furthermore, landscape fragmentation is a direct contributor to the removal of the natural honeybee habitat, fragmentation and subsequent isolation of the landscapes which the bees utilize for foraging (Cane & Tepedino, 2001). Moreover, fragmented landscapes can also result in nutritional deficiency for the honeybees since the nectar and pollen which the honeybees use as protein and energy sources are a function of flower availability in the landscape (Naug, 2009).

In Kenya, beekeeping is widely practiced and holds great promise for sustainable livelihoods especially in the arid and semi-arid regions (Carroll, 2006). It is estimated that only one fifth of the country's potential for honey and beeswax production is currently being exploited (GOK, 2008). Besides this, there is documented evidence that pollination services in the region are in decline, partly due to the growing dietary demands as a result of increasing human population, which results in more conversion of natural lands to cultivated lands (IPBES, 2016; Vaudo et al., 2012). Further, Kenya, like other countries in Africa is experiencing the effects of climate change and variability, with increased mean annual temperatures affecting ecosystems and consequently bee forage availability (Government of Kenya, 2016).

Whilst studies have been carried out in Kenya to examine the effect of proximity to forests on honey productivity (Sande et al., 2009) and effects of land cover on crop pollination (Gemmill-Herren & Ochieng, 2008), none of these studies have specifically examined the effect of landscape

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fragmentation metrics on honeybee colony strength. Yet there is a definite need for the quantification of landscape fragmentation metrics that could be explicitly linked to honeybees health, available forage resources, and other ecological, biological and nutritional requirements of honeybees. One of the major stumbling blocks in the research efforts for honeybees in the region is that there has been unavailability of freely available moderate to high resolution landscape maps until recently (Sudmanns et al., 2019). Fortunately, recent advances in space technology have availed earth observation data which have combined improved spatial and temporal resolutions. These data now have the potential to map landscape zones which are relevant to honeybees such as small grassland areas, residual natural and semi-natural vegetated areas and hedges (Hansen & Loveland, 2012; Malenovský et al., 2012). This study will therefore fill this important gap in knowledge by fusing newly available synthetic aperture radar (SAR) data and optical remotely sensed data so as to accurately map land cover, specifically those elements that are relevant to honeybees. Honeybee colony strength measurements will thereafter be carried out during key seasonal periods and subsequently, the linkage between landscape fragmentation, honeybee colony strength, pollen diversity and presence of *Varroa destructor* mite will be established.

1.3 Study aim and objectives

The overall objective of this work was to study the effect of landscape fragmentation on honeybee colony strength in Mwingi area, eastern Kenya. Fragmentation metrics were derived from a comprehensive mapping exercise of the area using space-borne remote sensing data while honeybee colony strength measurements were collected in five data collection exercises during key seasonal periods.

The following objectives were examined:

1. To derive novel landscape fragmentation indicators from newly available earth observation datasets.

2. To determine effects of landscape fragmentation on honeybee colony characteristics (adult population of worker bees, amount of brood, honey, pollen and eggs) at representative apiaries.

3. To establish pollen sources for honeybees as well as pollen nutritional content at and around representative hives.

4. To assess *Varroa destructor* effects on honeybee's colony strength as well as to determine the effects landscape fragmentation on *Varroa destructor*.

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1.4 Research scope of the study

This study investigates the linkages between landscape fragmentation and honeybee colony strength in an agroecological landscape in Kenya. Two major approaches were applied: 1) mapping of fine-scaled honeybee habitats and 2) collection of honeybee colony strength data. Fusion of SAR and multi-spectral remote sensing data from two spaceborne sensors (Sentinel-1A and Sentinel-2A) was applied for improvement of mapping accuracies. Thereafter, honeybee colony strength data was collected and interpreted using the Liebefeld method of estimation of honeybee colony strength parameters. Further, pollen in the form of bee bread was collected during data collection exercise for purposes of evaluation of plant diversity usage by the honeybees. *Varroa destructor* data was likewise collected from colonized hive at each visit. The Varroa ectoparasite was selected for evaluation since it has been shown to be the most destructive pest of honeybees. The linkages between the separate components of the study as conceptualized is shown in Figure 1.1

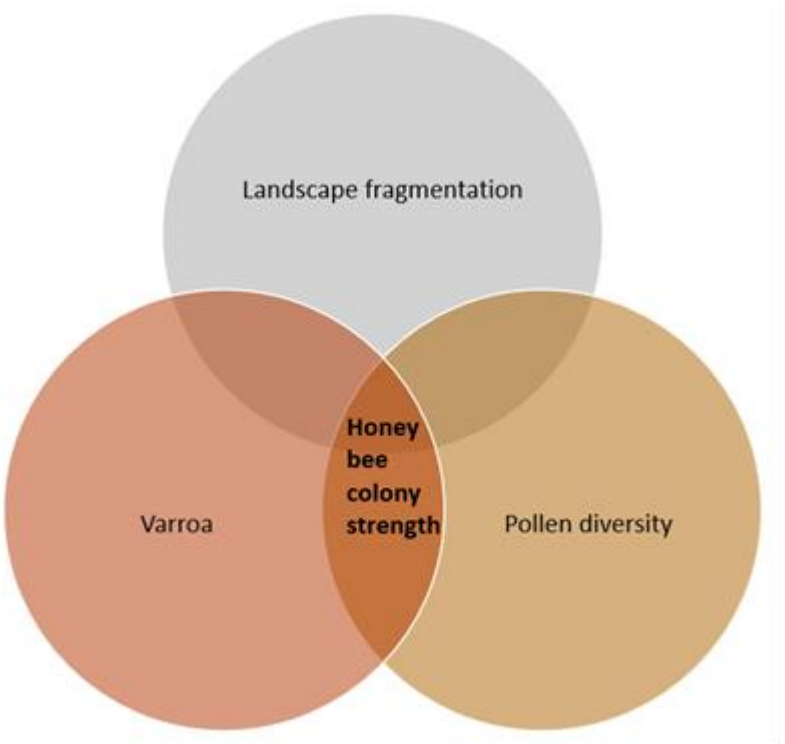

Figure 1.1: Linkages between the various components of the research study

1.5 Description of the study area

The study region is located in Mwingi sub-county within the greater Kitui County, in the eastern part of Kenya (Figure 1.2), ~ 150 km towards the north east of Nairobi. Mwingi area is recognized as a

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beekeeping region whose farmers have a long association of cooperation with agricultural research partners (Mburu et al., 2015). The region consists of largely heterogeneous landscapes, mainly composed of farmlands, shrublands, woody vegetation and grasslands. The region exhibits a semi-arid climate with a bimodal rainfall pattern whereby the long rainy season occurs between March and May and the short (but more reliable) rainy season occurs between October and December (Ngugi, 1999).

The annual average rainfall in the Mwingi study region ranges between 500 and 700 mm whereas the mean temperature ranges between 15 and 31 ºC. Six apiaries were established in the area within a bounding extent of ~ 3773 km^2.

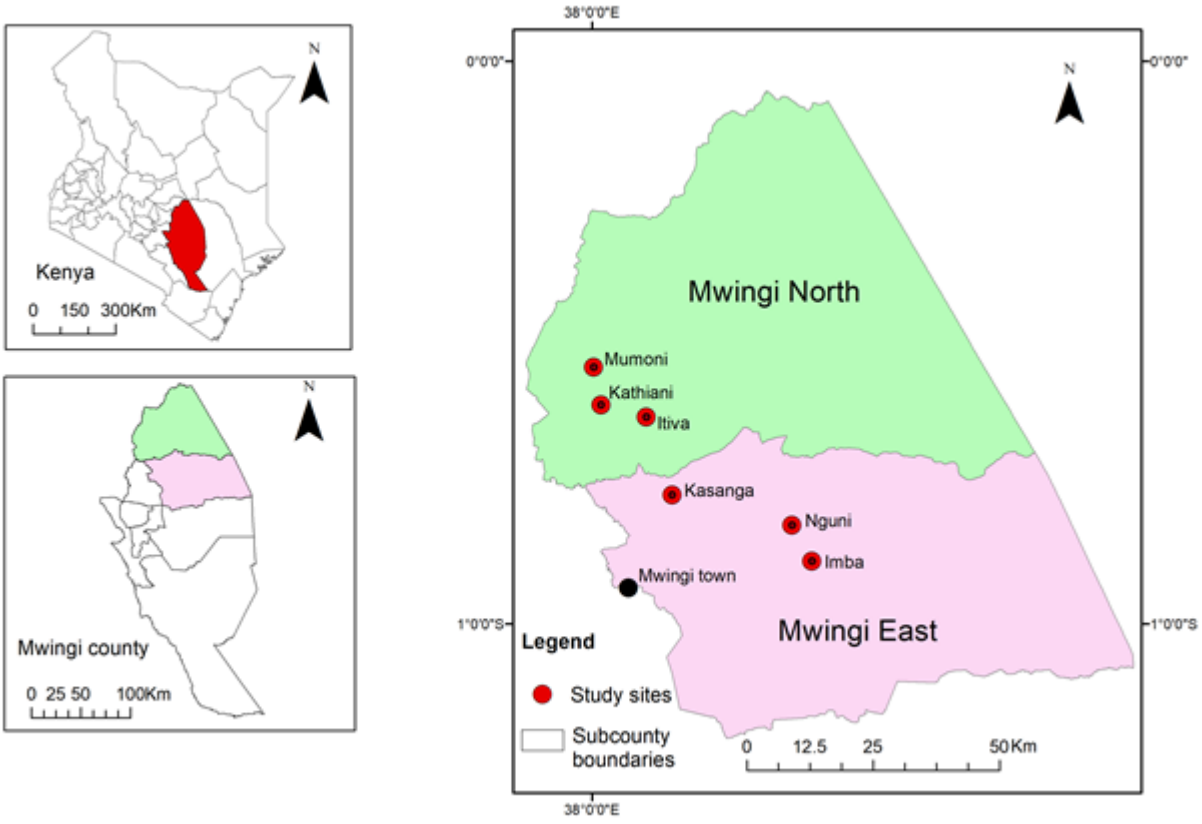

Figure 1.2: Location of the study area in Mwingi subcounty, Kenya

1.6 Thesis structure

The dissertation is structured in the form of chapters, whereby each objective forms an independent chapter, and the last chapter presents a synthesis of the previous chapters.

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Chapter 1 – General introduction

Honeybees are widely regarded as the world's most important pollinators mostly because of their large numbers and hence ability to pollinate vegetation and crops efficiently. However, there is a reported decline in their population, and this is linked to several factors, key among them, landscape characteristics. This introductory chapter demonstrates the need to understand the linkages between changes in landscape characteristics and honeybee colony strength. It provides important information as to how these changes can affect honeybees and the consequent effects on the ecosystem and humans. The chapter provides a justification of the study as well as its significance. Additionally, a detailed examination of the study objectives and overview of the methodological approach are presented.

Chapter 2 – A multi-sensor approach for mapping honeybee habitats in fragmented agroecological systems in Kenya

The increasing availability of moderate-to-high spatial and temporal resolution earth observation systems have enabled the quantification of landscape structure with higher accuracy than was previously possible. Mapping of honeybee habitats in this fragmented agroecological region has been carried out using newly and freely available optical and radar satellite data. Relevant fragmentation metrics have thereafter been generated, which demonstrates the differences in fragmentation patterns across the study sites.

Chapter 3 – Fragmented landscapes affect honeybee colony strength at diverse spatial scales in agroecological landscapes in Kenya

In Africa, anthropogenic activities have resulted in great changes to the spatial patterns of the natural landscape, resulting in altered configuration and composition of whole landscapes. This chapter examines the relationship between the landscape fragmentation parameters that were generated in the previous chapter, and honeybee colony strength data which are collected at six study locations distributed across varying landscape degradation gradients in the sub-county during five data collection periods. Specifically, the chapter explores the linkage between the fragmentation metrics and honeybee colony strength using zero inflated negative binomial mixed effects models.

Chapter 4 – Pollen diversity and nutritional content in differentially degraded semi-arid landscapes in Kenya

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It has been previously demonstrated that the availability and diversity of pollen, both on a spatial as well as temporal scale, helps determine honeybee foraging behaviour and therefore their productivity. This chapter examines the pollen diversity across the six variably fragmented study sites. Light microscopy methods are used to reveal the diversity of species which are used by honeybees across different landscapes. Further, protein content of pollen is assessed across locations and seasons. Alpha and beta diversity indices are assessed throughout the six study sites. The information generated in this chapter is very useful for conservation purposes, by revealing the plant species which honeybees prefer, as well as revealing the relationship between landscape degradation and pollen diversity in this region.

Chapter 5 – Does the presence of *Varroa destructor* influence honeybee colony strength in fragmented landscapes?

The *Varroa destructor* is a well-known honeybee pest which forms part of a multiple structure of stressors that may affect honeybee health in different ways. Globally, the mite is considered the most important threat to the apiculture industry. This chapter examines the linkage between Varroa mite presence and both honeybee colony strength and landscape fragmentation. Binary logistic regression models and zero inflated negative binomial mixed effects models are used to determine these linkages.

Chapter 6 – Landscape fragmentation, honeybee colony strength, pollen diversity and *Varroa destructor* presence: A synthesis

The overall findings of the thesis objectives are inferred from the previous chapters and summarized in this chapter. A comprehensive synthesis of the work and its contribution towards establishment of the value of the agroecological landscape for beekeeping in Kenya is elucidated. Relevant recommendations to policy and conservation are discussed. Suggestions for future research on the landscape effects on honeybee colonies in Kenya are also given.

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2 CHAPTER TWO: MULTI-SENSOR MAPPING OF HONEYBEE HABITATS AND FRAGMENTATION IN AGROECOLOGICAL LANDSCAPES IN KENYA

This chapter is based on:

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Presented at the 38th annual **European Remote Sensing Laboratories (EARSeL) Symposium**, Chania, Crete, Greece, July 10th 2018.

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Abstract

Extensive land transformation leads to habitat loss, which directly affects and fragments species habitats. Such land transformations can adversely affect fodder availability for bees and thus colony strength with consequence for rural communities that use bee keeping as a livelihood option. Quantification of the landscape structure is thus critical if the linkages between the landscape and honeybee colony health are to be well understood. In this chapter, a random forest algorithm was used on dual-polarized multi-season Sentinel-1A (S1) synthetic aperture radar (SAR) and single season Sentinel-2A (S2) optical imagery to map honeybee habitats and their degree of fragmentation in a heterogeneous agroecological landscape in eastern Kenya. The dry season S2 optical imagery was fused with the S1 data and class-wise mapping accuracies (with and without radar) were compared. Relevant fragmentation indices representing patch sizes, isolation and configuration were thereafter generated using the fused imagery. The fused imagery recorded an overall accuracy of 86% with a kappa of 0.83 versus the SAR imagery only, which had an overall accuracy of 76% with a kappa of 0.68. However, the S1 imagery had slightly higher user's and producer's accuracies for under-represented but important honeybee habitat classes, i.e. natural grasslands, and hedges. The variable importance analysis using the fused imagery showed that the short-wave infrared (SWIR) and the red-edge (RE) waveband regions were highly relevant for the classification model. Our mapping approach showed that fusing data generated from S1 and S2 with improved spectral resolution, could be effectively used for the spatially explicit mapping of honeybee habitats and their degree of fragmentation in semi-arid African agroecological landscapes.

Keywords: landscape structure, Sentinel 1 & 2, image fusion, Random Forest, honeybees, Kenya

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2.1 Introduction

A major contributor to the reported decline in pollinator species is changes in land use and land cover (Aizen & Feinsinger, 1994; Goulson et al., 2008; Potts et al., 2016), whereby changes in landscape configuration are thought to be the main causes of the decline of pollination services within agricultural systems (Viana et al., 2012) Anthropogenic activities have drastically altered the natural habitat through fragmentation and degradation of the environment leading to destruction and the emergence of new man-made habitats which ultimately influence pollinators, their preferred plants as well as their interactions at all scales (Kremen et al., 2007).

The loss of natural habitats as well as habitat fragmentation poses a threat to bee populations, particularly because of land transformation for agricultural expansion (Vaudo et al., 2012). This directly contributes to removing the natural bee habitat, and fragments and hence isolates the land in which the honeybees travel across and forage on (Cane & Tepedino, 2001). Also, it is found that habitat fragmentation can reduce gene flow among bee populations, which leads to a reduction of genetic diversity within the populations and, therefore, increased inbreeding (Kremen et al., 2007). Further, in the case of honeybees, habitat fragmentation could lead to nutritional deficiency since the flora in the habitat provide nectar and pollen which are food source for the bees, thereby habitat fragmentation can affect the survival rates for both the adult bees as well as the brood (i.e., bee larva) (Naug, 2009). Therefore, there is a need to identify landscape habitats and fragmentation variables that could be explicitly related to honeybee health, diversity, foraging behaviour and other honeybees' nutritional, biological and ecological related needs.

The increasing availability of earth observation data with high spatial and temporal resolutions have a vast potential to map landscape habitat zones that are more relevant to pollinators such as hedges and residual pockets of natural vegetation, (Hansen & Loveland, 2012; Malenovský et al., 2012). Earth observation data, that are commonly more cost-effective over wider areas than on-site field survey, can also be effectively utilized to assess landscape fragmentation in semi-transformed landscapes at finer scales (Kerr & Ostrovsky, 2003; Stratoulias et al., 2015). Moreover, earth observation products like normalized difference vegetation index (NDVI), leaf area index (LAI) and fraction of photosynthetically active radiation (fPAR) are increasingly being used to study and map landscape ecological processes and patterns (Galbraith et al., 2015). Whereas earth observation optical sensors have been the major source of land cover and land structure information, including landscape classes and fragmentation for several decades (Laurin et al., 2012), certain issues can affect the ability of these optical sensors to provide comprehensive and quality data throughout the seasons. For instance, tropical regions suffer from persistent cloud cover during the rainy seasons (Laurin et

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al., 2012) that affects the ability of the optical sensors to capture good quality cloud-free data. Synthetic Aperture Radar (SAR) has in recent times emerged as an important data source system which enables mapping of landscape classes and assessing their level of fragmentation even when atmospheric conditions are unfavourable, due to the ability of SAR data to penetrate clouds (Lehmann et al., 2012) as well as independence to sun-induced reflection (Hütt et al., 2016). Whereas SAR satellite systems present a wide variety of selectable configurations (polarization, the incidence angle, and spatial resolution), optical systems only operates in a single configuration imaging mode (Hütt et al., 2016). However, the improved spectral configuration of the relatively newer optical sensors in critical waveband regions such as the red edge showed an improved model performance for mapping landscape classes in semi-arid regions (Li et al., 2017; Schumacher et al., 2016). Likewise, several studies reported improved accuracies for mapping landscape classes by adopting synergistic approaches involving SAR and optical sensors, with various fusion algorithms. Torbick et al. (2017) fused Landsat 8 OLI, PALSAR and Sentinel-1A (S1) images for land use/ land cover (LULC) mapping in Myanmar and found that very high overall as well as kappa accuracies resulted from the fusion of these datasets. On the other hand, Clerici et al. (2017) and Chatziantoniou et al. (2017) fused S1 and Sentinel-2A (S2) images for LULC and wetland mapping, respectively and reported improved LULC and wetland mapping accuracies as a result of integrating S1 and S2 data sets.

In Africa, landscape heterogeneity caused by a mixture of overlapped LULC classes, increases the complexity and difficulty of mapping fine-scale honeybee habitat zones (Marston et al., 2019). Habitats like hedges, grasslands or their transition zones, semi-natural and natural vegetation pockets are all important for honeybees (Donkersley, 2019; Gallant et al., 2014; Requier et al., 2015), particularly because they provide pollens and nectar during different times of the season. In addition, Some of these habitats and their fragments like small and large forest fragments are critical to the survival of the bees, while others like hedges act as corridors for the movement of the bees and prevent isolation of the natural habitat patches by improving the connectivity of these patches (Brosi et al., 2008; Krewenka et al., 2011). Therefore, the ability to accurately map these landscape habitats enables the analysis of the degree of landscape fragmentation, which then gives an indication of landscape integrity and suitability for honeybees wellbeing (Brosi et al., 2008b).

On the other hand, studies have also looked at the possibilities of using spatial modelling approaches to assess the impact of the surrounding habitats on the status of bees' health. For instance, Koh et al. (2016) estimated an index of bee abundance across the coterminous United States and found that areas surrounded by intensive agricultural systems had the lowest bee abundances. Further, Olsson et al. (2015) modelled pollinating bees visitation behaviour in heterogeneous landscapes using both the

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Lonsdorff and the Central Place Foraging (CPF) models. The study showed that the wellbeing of the bees was negatively correlated with the distances that they would have to travel to access quality foraging resources.

To the best of my knowledge, no comprehensive mapping of honeybee habitats and their fragments has been carried out in agroecological landscapes in semi-arid Africa. Sande et al. (2009) assessed the levels of honey production with an increasing isolation from forested areas in Kenya. However, this study measured only the distance from 'forest' and did not use earth observation methods, which consider the entire land cover characteristics especially the configuration and composition of the landscapes. Agroecological landscapes in Africa are typically a mosaic of residual pockets of near-to-natural vegetation and croplands. Moreover, agroecological landscapes are rapidly changing due to land transformation processes (Hooke & Martín-Duque, 2012). In this chapter, the key question asked was: can landscape variables from remote sensing be used to quantify the potential of the landscape matrix for successful honeybee colonies? Hence the recently available optical and SAR Sentinel imagery from the European Space Agency (ESA) were utilized for their potential to provide fine-scaled spatial information feeds on land cover/ use classes (features) and landscape fragmentation metrics relevant to honeybees colony strength. Specifically, the use of S1 SAR data, S2 optical data and fused S1-S2 data together with advanced machine learning random forest classification algorithm were explored for mapping honeybee habitats and their fragmentation status in agroecological landscapes in eastern Kenya. This synergistic landscape habitat mapping approach is unique since it makes use of the imaging capabilities of the S1 SAR data and the particular spectral characteristics of the S2 data (Adamo et al., 2013).

2.2 Methods

2.2.1 Study area

The study region lies in Mwingi sub-county (an important honeybee keeping area) within the greater Kitui County, in the eastern part of Kenya (Fig. 1), approximately 150 km towards the north east of Nairobi. The region exhibits a semi-arid climate with a bimodal rainfall pattern. The long rainy season occurs between March and May and the short but more reliable rainy season occurs between October and December (Ngugi, 1999). The annual average rainfall in the Mwingi study region ranges between 500 mm and 700 mm whereas the mean temperature ranges between 15 ~ 31 °C. Six study sites were chosen as honeybee apiary locations within the study region, and are within an extent of approximately 3773 km².

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The six study sites were selected for honeybee apiary placement based on three 'land degradation severity' gradients, typical for the study region (Fig. 2.1) related to the abundance and proportion of natural vegetation in each site. The 'land degradation severity' gradients were predefined from field observations that revealed extensive land degradation in varying degrees, particularly increasing in the south eastern parts of the study area: (1) An abundance of natural vegetation characterizes the two 'least-degraded' sites (Mumoni and Kathiani), (2) the two 'mixed cropland and natural vegetation' sites (Kasanga and Itiva Nzoo) consisted of cropland interspersed with natural trees, and (3) the two 'degraded' sites (Nguni and Imba) were composed of very little near to natural vegetation. Overall, agricultural activities have produced markedly fragmented landscapes in the region, and illegal logging activities are carried out for charcoal burning purposes. The diversity and heterogeneity of available landscapes within Mwingi provided a suitable environment in which to carry out the study, since the specific effects of the habitat on honeybees can be elucidated in addition to the fact that the Mwingi region is a traditional bee-keeping area.

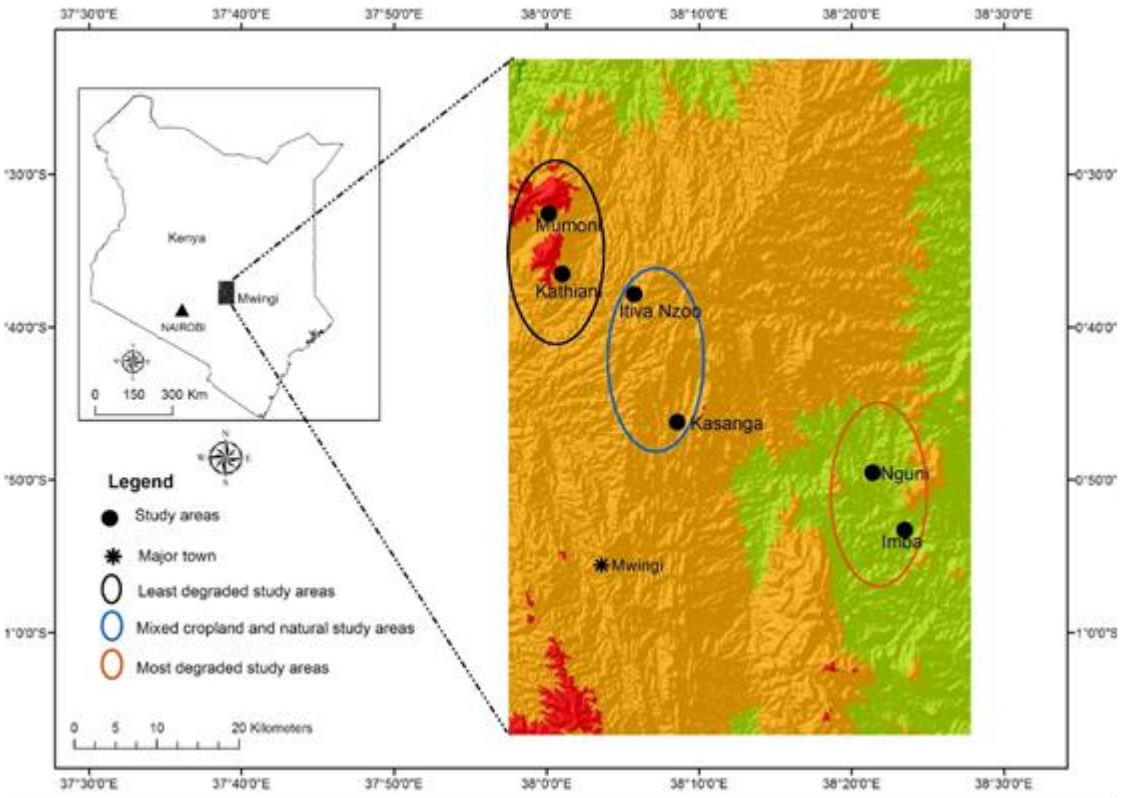

Figure 2.1: Location of the study region in Kenya (left) and the three 'land degradation severity' areas, indicated as ellipsoids. The green, orange, and red shades show low, medium, and high elevation, respectively (http://dds.cr.usgs.gov/srtm/)

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2.2.2 Satellite data acquisition and pre-processing

Sentinel-1A

Sentinel1 imagery for the study region was acquired from the European Space Association (ESA) Copernicus Open Access Hub (ESA, 2017). The S1 platform follows a Sun-synchronous, near-polar, circular orbit at a height of 693 km and a repeat cycle of 12 days at the equator (Torbick et al. 2017). S1 C-band SAR images, in ascending orbit with incidence angle between 20º and 45º were acquired in the Interferometric Wide Swath (IW) mode with a single look 250 km swath at a ground range of 5 m by 20 m (Torres et al. 2012). The acquisition was carried out for two key periods that corresponded to the key vegetation phenological seasons in the Mwingi region, which were on the 10th September 2015 (peak dry season) and on the 9th December 2016 (peak short rainy season). S1 images were dual polarized in 'Vertical Transmitted-Vertical Received' (VV) and 'Vertical Transmitted-Horizontal Received' (VH) mode. The pre-processing procedures consisted of the standard SAR routines, including radiometric calibration, S1 Terrain Observation with Progressive Scans (TOPS) deburst and terrain correction as well as resampling to 10 m spatial resolution using Range-Doppler correction method with 90 m elevation data from the Shuttle Radar Topographic Mission (SRTM) digital elevation model (Jarvis et al., 2008). All pre-processing was done within the Sentinel Application Platform (SNAP) software (ESA, 2017). Both images were subset to the extent of the study sites and then stacked together into one image comprising the four dual polarized bands (i.e. two for each acquisition date).

Sentinel-2A

A single-season top-of-atmosphere (TOA) S2 level 1C image for the dry season (30 August 2016) was acquired from the ESA Copernicus Open Access Hub (European Space Association (ESA), 2017). The S2 sensor carries a multispectral imager with a swath width of 290 km together with 13 spectral bands in the visible, near infrared, red edge and shortwave infrared parts of the spectrum (ESA, 2017). All the available S2 imagery for the study region specifically during the wet seasons (March to May and October to December) from the years 2015 to 2017 had very high levels of cloud cover (above 30%) and hence were deemed unsuitable for use in this study. Thus, only one dry season S2 image could be pre-processed and used in this study. The S2 image was atmospherically corrected using the Sen2cor module within SNAP and then subset to the study area extent. All bands were then re-sampled to 10m X 10 m pixel size using the bilinear interpolation method to achieve the same

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resolution across all the bands and to have the same resolution as in S1 imagery. Bands 1, 9 and 10 (coastal aerosol, water vapor and cirrus, respectively) were excluded altogether from the analysis.

S1 and S2 data fusion

Earth observation systems capture spectral data in different portions of the electromagnetic spectrum (EMS) like the optical and SAR systems provide complementary spectral data. Hence, fusing S1 SAR and S2 optical data sets offers additional information that are necessary for accurately mapping and delineation of landscape features that are, for instance, important honeybee habitats (Kuchma, 2016; Sandberg, 2016). Specifically, the concept of image fusion refers to the process of acquiring and synergistically integrating information which originates from different image sources to derive more information from a composite image (Amarsaikhan et al., 2007; Simone et al., 2002; Brahmbhatt and Makwanna, 2013).

In this chapter, the dual polarized and stacked S1 imagery for the two seasons were fused with the single season S2 image using the collocate tool in the SNAP 5.0 tool, following a pixel-to-pixel fusion approach (Pohl and Van Genderen, 2010). In the fusion process, the band data of the S1 images were resampled onto the geographical raster of the S2 using the bilinear interpolation method, whereby the geo-position of the master raster (S2) was used to find the corresponding position of the slave raster (S1 composite). All the components of the master and slave rasters were copied, but only the metadata for the master raster were transferred.

2.2.3 Mapping honeybee habitats in a landscape scale

Reference data collection

Four classes that were deemed relevant for honeybee habitats and representative for the study area landscape were identified based on their ability to provide foraging resources for the bees: woody natural vegetation (Donkersley, 2019), natural grasslands (Gallant et al., 2014) , hedges (Donkersley, 2019) and cropland (Requier et al., 2015). In addition, three other landscape classes, *viz*, water bodies/bare soil, built-up/ rock which were in the study area were identified and sampled as reference classes to avoid the confusion between these classes and some of the honeybee habitats. The water bodies/ bare soil classes were combined because the rivers in the area are seasonal and reflect the same as bare soil, while the built-up/ rock classes were also combined for the same reason. The croplands were separated into ‘cropland-on’ and ‘cropland-off’ categories to be able to map ‘in or out

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of the growing season' crops but were later combined after classification into one 'cropland' class. The training signature reference data for the classification were collected from a Google Earth platform with a high spatial resolution image captured on 15 June 2016. A random sampling approach was followed to collect the training signature reference data across the study area, whereby a total of 456 polygons (*n* = 1945 pixels) were selected as training samples. These were distributed as 160 polygons (*n* = 173 pixels) for hedges class, 103 polygons for built-up/ rock class (n = 276 pixels) and 30 training polygons for each of the woody vegetation (*n* = 616 pixels), water bodies/bare soil (*n* = 340 pixels), 'cropland-off' (n = 185 pixels) 'cropland-on' (n = 115 pixels) and grasslands (*n* = 240 pixels) feature classes (Fig. 2.2). Since the hedges and built-up/rock features are fine-scaled features as compared to other classes, we sampled more polygons to increase the representation of their signature in the classification experiment. The sample training classes were dispersed randomly across the landscape gradients to enable the collection of robust and representative training as well as validation datasets. The reference data were divided into two parts: training set (70%) and a validation set (30%) based on a recommendation by Adelabu et al. (2015).

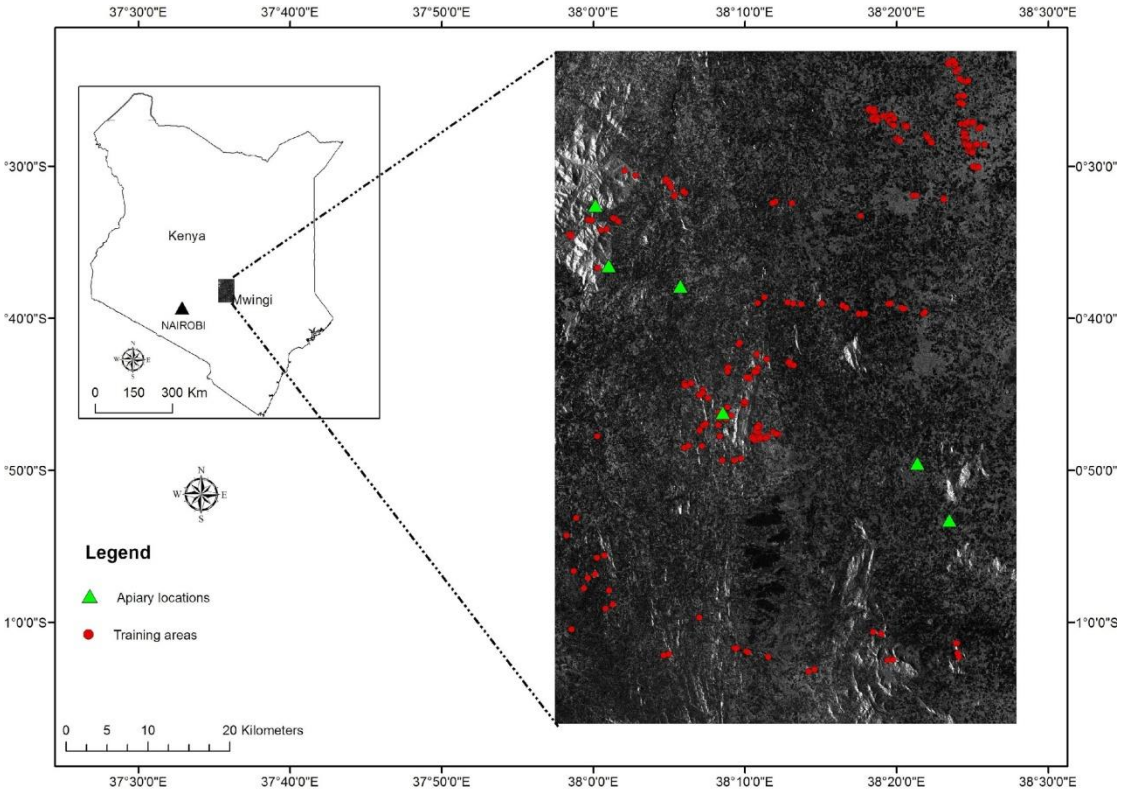

Figure 2.2: Map showing location of sites where reference data was collected in the study region overlaid on Sentinel-1A (S1) Vertical Transmitted-Horizontal received (VH) polarized image. Reference data collection sites are displayed in red colour while the six honeybee apiary location sites are displayed as green triangles.

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Random forest (RF) classification

A pixel-based Random Forest (RF) classifier (Breiman, 2001) was performed to map the honeybee habitats in the study area using S1, S2 and fused S1- S2 imagery. RF was used in this study since it is a flexible, efficient and powerful non-parametric machine learning algorithm that is robust against over-fitting, outliers and can handle thousands of input variables (Breiman, 2001; Horning, 2010). Additionally, RF is a very straightforward classification method since it mainly requires setting of only two parameters. These are the randomly selected number of variables used to split each decision tree in the forest at every node (*Mtry*), and the number of decision trees in the forest (*Ntree*). In a classification application, each decision tree votes for a class membership and the final outcome is determined by the maximum votes of the decision trees (Belgiu & Dragut, 2016; Breiman, 2001). Additionally, RF produces a variable importance by-product that ranks the input predictor variable according to their importance in separating the classes in the experiment. In this study, *Ntree* was set at the default value of 500 which has been shown to be suitable for stabilizing the internal classification error (Belgiu & Dragut, 2016). The default *Mtry* value which is the square root of the number of variables was used. Three classification exercises were employed to map the honeybee habitats and other LULC classes using the RF algorithm: (1) classification of the combined wet and dry seasons S1 images, (2) classification of the single season S2 image, and (3) classification of the fused S1-S2 image. Ranking of the fused S1-S2 bands was also carried out according to their importance in increasing the overall classification accuracy of mapping the honeybee habitats using the RF variables importance by-product.

Classification accuracy assessment

Classification accuracy was assessed for all landscape maps that were produced using S1, S2, and fused S1-S2 data sets. Classification confusion metrics, *viz*, overall accuracy (OA), user's accuracy (UA) and producer's accuracy (PA) as well as kappa coefficient were calculated and used as criteria for maps accuracy assessment. To test whether there were any significant differences among the landscape mapping results for the three classification experiments (S1, S2, and fused S1-S2 data), a McNemar's chi-square test was carried out based on the formula suggested by de Leeuw et al. (2006) and Foody (2004). In addition, for the fused S1-S2 data, each honeybee habitat class was perturbed three times and the percent correct predictions for a landscape classes were averaged. Thereafter,

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within-class and between-class variabilities were computed to determine whether the classes were separable from each other at each band to ascertain the most relevant spectral bands. Further, boxplots and mean reflectance and backscatter values at each band for the classes were used to display the within-class variability; and a Tukey test ($p \leq 0.05$) of the analysis of variance (ANOVA) was used to determine the between-class separability.

2.2.4 Deriving fragmentation indices

Fragmentation indices for the honeybee habitats were extracted from the landscape map that was produced using the fused S1-S2 image because it had the highest OA classification accuracy. These metrics were derived to quantify the landscape structure by configuration, size, shape, number of patches and their position within the landscape (Jung, 2016). The FRAGSTATS tool (Mcgarigal, 2014) was selected for this process since it calculates fragmentation metrics at the individual class (several patches of the same class) and landscape level (Mcgarigal, 2014). An apiary was located in each of the six study sites and used as a central point to create a buffer of 3 km radius around each study site. The buffers were utilized to extract the fragmentation indices. The selected 3 km radius for the buffers were based on the honeybees foraging distance which was estimated to be within 3 km from an apiary (Hepburn, and Radloff, 1998; Roubik, 1989). To derive fragmentation indices using FRAGSTATS tool, a spatial resolution of 1-meter for a classified map is required (Mcgarigal, 2014). Hence, the most accurate landscape map within the buffer zones was resampled to 1-meter spatial resolution and derived the fragmentation indices for each of the six test sites.

Class and landscape-level fragmentation metrics were thereafter derived. Landscape fragmentation was assessed by considering indices that describe patch size, shape and configuration (Rutledge, 2003), mainly because linkages between these indices and ecological processes are perceived to be relatively clear, and these indices are commonly used to quantify the changes in landscape configuration usually associated with habitats loss and fragmentation (Kupfer, 2012). The derived class and landscape metrics are described in Table 2.1.

Table 2.1: Class and landscape fragmentation indices used in this study (Mcgarigal, 2014)

Index type	Fragstat index	Description
	Class	
Landscape composition	Percentage of landscape (PLAND)	The proportional abundance for each of (PLAND) the patch types across the landscape

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Landscape configuration	Largest patch index (LPI)	An index used to quantify the percentage of total landscape area characterized by the largest patch
Landscape shape	Landscape shape index (LSI)	An index used to reflect the complexity of the landscape patches; a greater value indicates more complexity
Landscape		
Landscape composition	Splitting index (SI)	Number of equal-sized patches of a specific class which is needed to produce a desired degree of landscape division
Landscape shape	Fractal dimension (FD)	Measures the degree of shape complexity
Landscape composition	Shannon diversity index (SHDI)	Measures the number of landscape elements as well as their proportional changes. Also, the abundance of landscape types.
Landscape connectivity	Contagion (CONTAG)	A measure of the degree of adjacency of classes within a map

2.3 Results

2.3.1 Honeybee habitats mapping in the landscape of the study area

Sentinel-1A images classification

Fig. 2.3 presents a landscape map in the study area using the combined wet and dry seasons S1 imagery. The map shows that S1 over-estimated the woody vegetation class at the expense of other feature classes.

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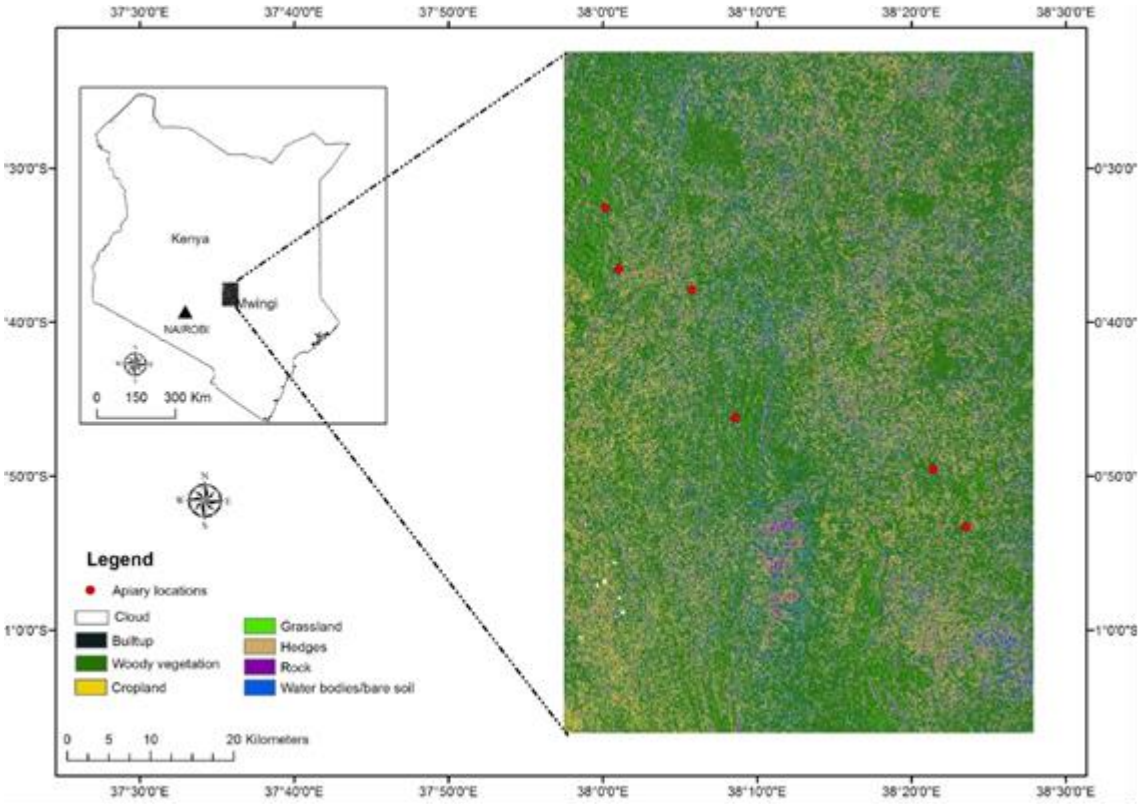

Figure 2.3: A landscape classification map of the Mwingi study region produced using the combined wet and dry seasons S1 images acquired in September 2015 and December 2016, respectively, using the random forest classifier.

The overall accuracy of the combined S1 map was 75.34% with a kappa coefficient value of 0.68 (Table 2.2). The S1 images detailed classification results are shown in Table (2.2) Specifically, Table (2.2) shows that among the four honeybee habitats, the woody vegetation class was mapped with the highest individual PA (76%), hedges with the highest UA (83%), while grasslands were mapped with the lowest PA (48.61%) and UA (67.31%). When compared S1 classification results with the other two classification experiments (S2 and fused S1-S2), the results further showed significant differences among the three mapping exercises using the McNemar's test (Table 2.5).

Table 2.2: Confusion classification matrix for the landscape classes in the Mwingi study region mapped using the combined S1 wet and dry seasons images acquired in September 2015 and December 2016, respectively, and using random forest as a classifier. PA = Producers' accuracy, OA = Overall accuracy

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	Woody	Cropland	Grassland	Hedges	Built-up/Rock	Water/ Bare	Total
Woody	**146**	7	20	14	4	1	**192**
Cropland	10	**71**	10	1	4	0	**96**
Grassland	17	0	**35**	0	0	0	**52**
Hedges	5	0	0	**26**	0	0	**31**
Built-up/ Rock	3	10	0	0	**71**	6	**90**
Water/Bare	4	2	7	11	4	**95**	**123**
Total	**185**	**90**	**72**	**52**	**83**	**102**	**584**
PA%	78.92	78.89	48.61	50	85.54	93.14	
OA%	76.03						
Kappa	0.68						

Sentinel-2A images classification

The map of the landscape classes in the study area produced using the single season S2 image is presented in Fig. 2.4. The map showed that croplands are well-distributed and a dominating class across the study region. As opposed to the map produced using S1 image, the overall accuracy of the S2 map had a higher overall accuracy (85.44%) and kappa statistic (0.82). The outperformance of S2 mapping results in comparison with S1 is further demonstrated by the McNemar's test result (Table 2.5) that indicated a significant difference between the two classification exercises. However, the difference between S2 and the fused S1-S2 classification experiments was not significant (Table 2.5). With regards to the individual UA and PA when S2 image was utilized, the woody vegetation habitat class achieved the highest UA (100%), as well as the highest PA (97.3%). Grassland and hedges honeybee habitat were mapped with a low PA (44.44% and 44.23% respectively), while croplands class had a moderate UA (53.85%) (Table 2.3). For the built-up/rock, bare and water landscape classes, the result of the S2 mapping experiment showed fairly higher UA and PA compared to the S1 classification results.

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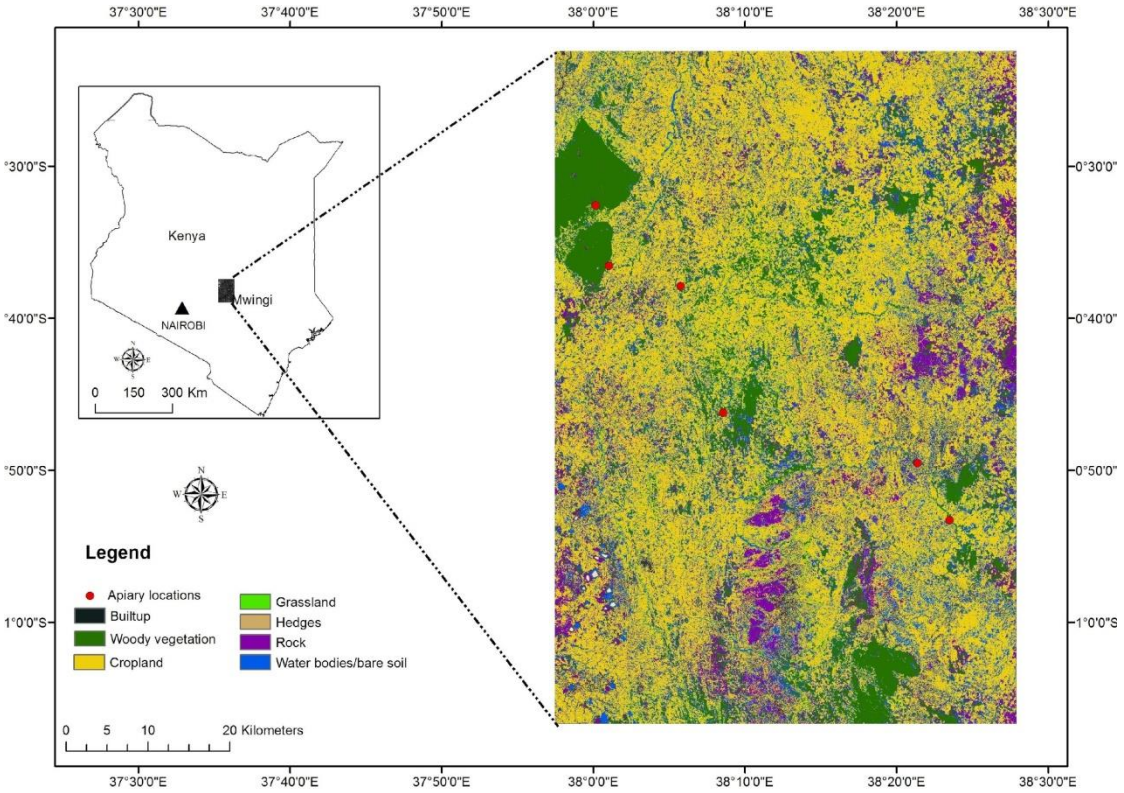

Figure 2.4: Classification map of the Mwingi study region produced using the single season S2 image acquired on 30 August 2016

Table 2.3: Confusion classification matrix for the classes in the Mwingi study region mapped using the single Sentinel-2A image acquired on 11 August 2016 and using random forest as a classifier. The columns of the table are the ground truth classes while the rows are the classes of the classified image that are being assessed. PA = Producers' accuracy; OA = Overall accuracy

	Woody	**Cropland**	**Grassland**	**Hedges**	**Built-up/ Rock**	**Water/ Bare**	**Total**
Woody	**180**	0	0	0	0	0	180
Cropland	1	**84**	38	28	0	5	156
Grassland	1	5	**32**	0	0	0	38
Hedges	0	0	1	**23**	0	0	24
Built-up/ Rock	3	0	0	1	**83**	0	87
Water/ Bare	0	1	1	0	0	**97**	99
Total	**185**	**90**	**72**	**52**	**83**	**102**	**584**
PA%	97.3	93.33	44.44	44.23	100.00	95.10	
OA%	85.44						
Kappa	0.82						

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Fused Sentinel-1A and Sentinel-2A image classification

The fused S1-S2 image classification produced the more accurate landscape map (Fig.2.5) for the study area as compared to the other two classification results (i.e. S1 and S2 classifications). The fused classification experiment showed great similarity to the S2 map with regards to the honeybee habitats but fewer rock outcrops towards the north-eastern part of the study area were mapped. The classification confusion matrix for the fused map is displayed in Table 2.4. The overall classification accuracy (86.43%, and kappa coefficient = 0.83) obtained using the fused S1-S2 data is higher than the results obtained when using the two S1 images or the S2 dry season image In the S1-S2 fused result, woody vegetation was the most accurately mapped habitat class (UA =97.29% and PA = 95.75%), while the hedges class had a low PA (42.41%) but high UA (100%). The other landscape classes (i.e. built-up, rock, bare and water) were mapped with individual accuracies of up to 100%. As mentioned earlier, the difference between landscape mapping results using the fused S1-S2 and S1 imagery was significant according to McNemar's test results, while the difference between the fused S1-S2 and S2 imagery was not significant (Table 2.5).

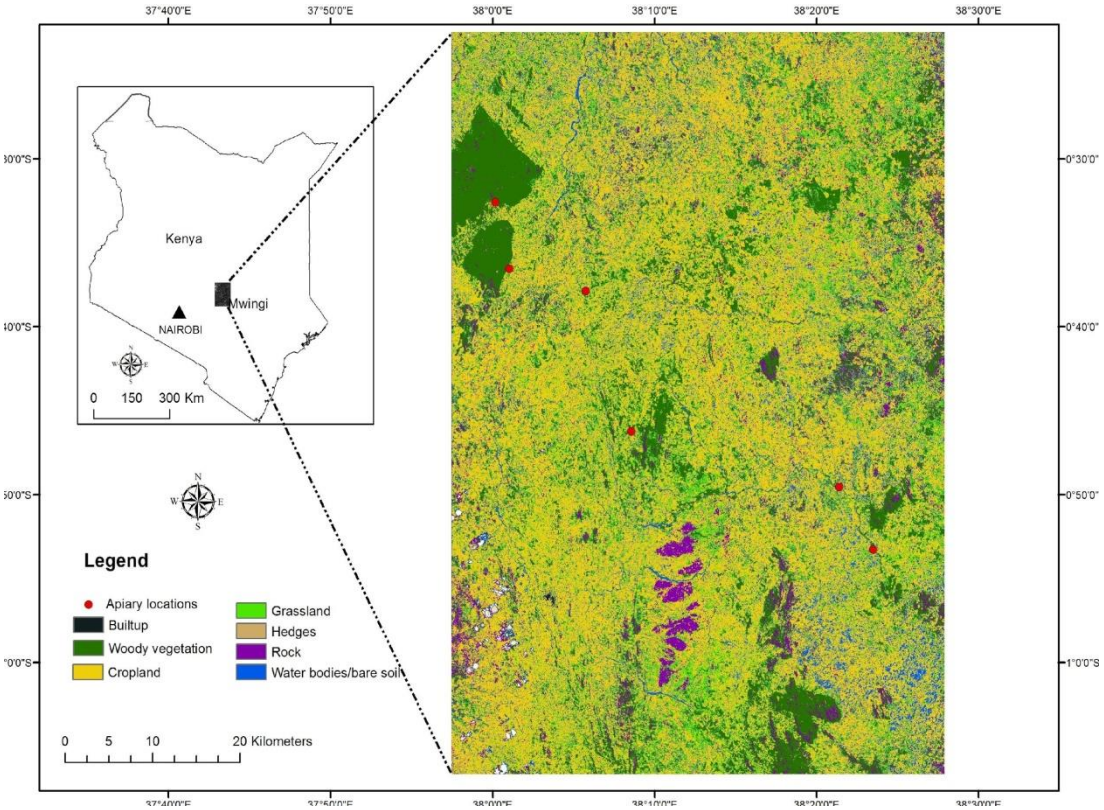

Figure 2.5: A landscape map of the Mwingi study region produced using the fused S1-S2 image and the random forest classifier

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Table 2.4: Confusion classification matrix results for landscape classes in the Mwingi study region using the fused Sentinel-1 and Sentinel-2 image and random forest as a classifier. The columns of the table are the ground truth classes while the rows are the classes of the classified image that are being assessed. PA = Producers accuracy; OA = Overall accuracy

	Woody	**Cropland**	**Grassland**	**Hedges**	**Built-up/ Rock**	**Water/ Bare**	**Total**
Woody	**180**	1	7	0	0	0	
Cropland	0	**86**	32	30	0	1	
Grassland	0	3	**33**	0	0	2	
Hedges	0	0	0	**22**	0	0	
Built-up/ Rock	5	0	0	0	**83**	0	
Water/Bare	0	0	0	0	0	**99**	
Total	**185**	**90**	**72**	**52**	**83**	**102**	
PA%	97.29	95.56	45.83	42.31	100	97.06	
OA%	86.43						
Kappa	0.83						

Table 2.5: McNemar's test results of comparing Mwingi study region landscape mapping results produced using the three classification experiments (S1, S2, and fused S1-S2 images)

Comparison	*p*-value	Chi-square (χ^2) value	Significance ($p \leq 0.01$)
S1 vs. S2	0.0001	91.84 (1df)	Significant
S1 vs. fused S1- S2	0.0001	79.507 (1df)	Significant
S2 vs. fused S1- S2	0.2976	1.085 (1df)	Not significant

df = degree of freedom

Fused Sentinel-1A and Sentinel-2A bands importance for mapping the studied honeybee habitats

Fig. 2.6 shows the importance of the fused S1-S2 image bands for mapping the landscape honeybee habitats in the Mwingi study region as determined by the RF variable importance by-product. The results showed that the most important band for classifying the landscape classes in Mwingi was SWIR (shortwave infrared), followed by RE (red edge), blue, and the VH bands, respectively. Only the VH band of the S1 image acquired during the wet season was selected as an important SAR feature for separating the landscape classes in the Mwingi study region.

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The intra and inter honeybee habitat variabilities in the four most important fused S1-S2 bands are shown in Fig. 2.7. The figure revealed the discriminability among the studied honeybee habitats as determined by the relatively higher inter classes variabilities. Also, the mean reflectance or backscatter values at each band are significantly different according to Tukey's test scores among the four honeybee habitats (Fig. 2.7). On the other hand, the relatively lower intra class variabilities in the four most important fused S1-S2 bands, confirmed that higher mapping accuracies could be achieved using the fused S1-S2 bands.

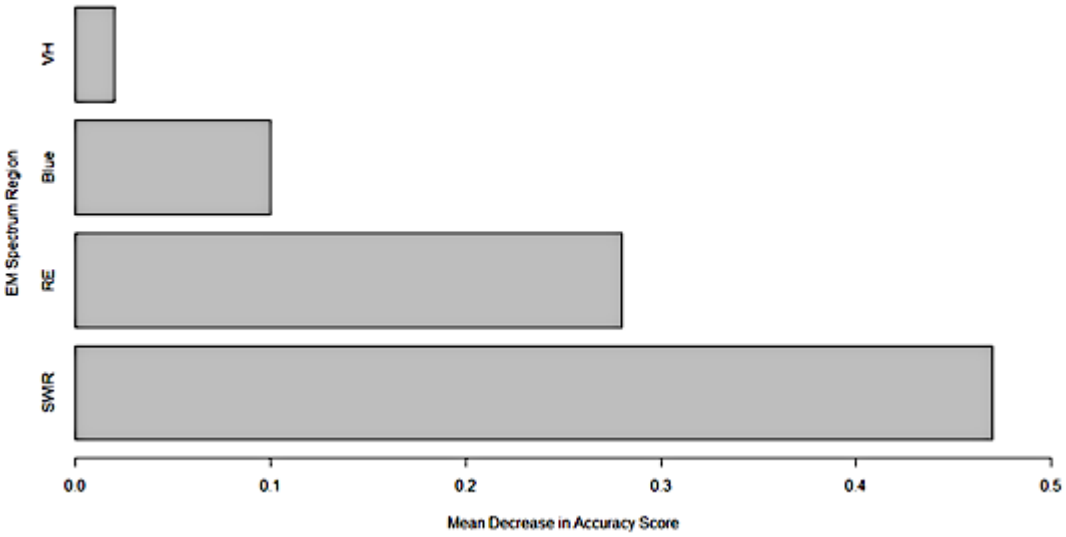

Figure 2.6: The importance of the fused Sentinel-1 and Sentinel-2 (S1-S2) bands for mapping the landscape classes in the Mwingi study region as determined by the random forest variable importance by-product. SWIR, RE, and Blue are shortwave infrared, red edge and blue bands of the electromagnetic spectrum, while VH is the vertically transmitted and horizontally received band in the Synthetic Aperture Radar (SAR) systems

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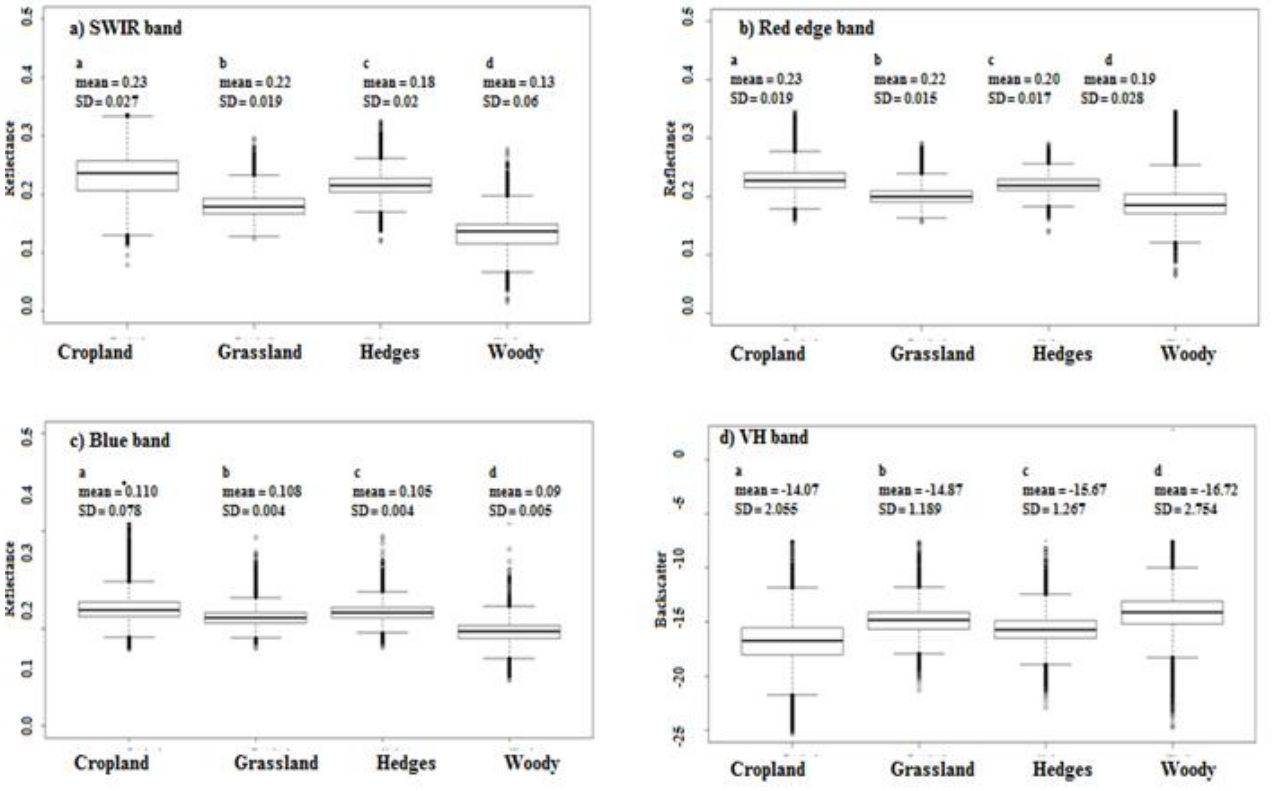

Figure 2.7: Boxplots distributions for each of the four most important fused S1-S2 bands for the four studied honeybee habitats: (a) Short wave infra-red (SWIR) (b) Red Edge, (c) Blue, and (d) Vertical Transmitted – Horizontal Received (VH). Individual data points are represented by asterisks. Mean reflectance or backscatter values for each class (represented by a boxplot) with different letter at each band were significantly ($p \leq 0.05$) different from each other according to the Tukey's test. SD is the standard deviation. See Fig. 6 for the meaning of SWIR and VH bands.

2.3.2 Fragmentation indicators

Landscape-level fragmentation

Results from the landscape-level fragmentation analysis using the fused S1-S2 landscape map reveal marked differences in fragmentation patterns among the six test sites in the Mwingi study region (Fig. 2.8). The figure demonstrates that Mumoni and Kathiani test sites had the lowest SI (1.6 and 5.1, respectively), while Imba and Nguni sites had the highest SI (93.2 and 88.5 respectively). This indicates that the latter sites were highly fragmented (Fig. 2.8a) and had fewer semi-natural areas (Fig. 8a) in comparison with the other test sites. Regarding landscape shape, the FD index (Fig. 2.8b) was lower in Mumoni (1.60) and Kasanga (1.61) and higher in Imba (1.66) and Nguni (1.67). The smaller the FD value, the simpler and less convoluted the landscape patch shape and vice versa. Concerning landscape connectivity, the results showed that Mumoni and Kathiani had the highest CONTAG index of 68.25 and 36.7, respectively (Fig. 2.8c), whereas, the Imba (18.83) and Nguni (17.33) had the lowest values (Fig. 2.10 c). The higher CONTAG index demonstrates higher

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landscape connectivity. Further, the low SHDI in Mumoni (0.77) illustrates its homogenous landscape as opposed to the other five test sites (Fig. 2.8d).

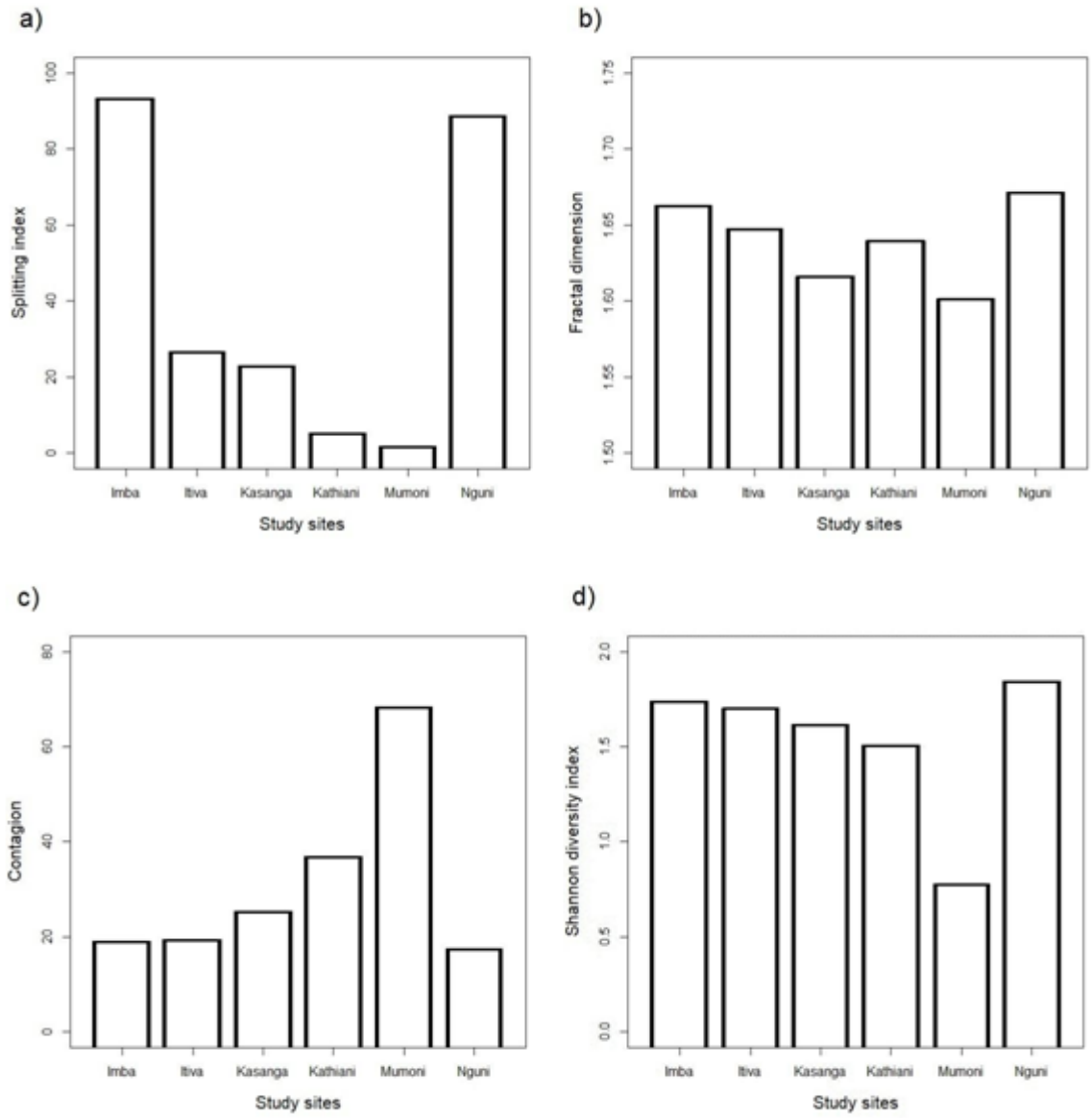

Figure 2.8: Mean landscape-level fragmentation indices in the six test sites in the Mwingi study region, Kenya: a) Splitting index, b) Fractal dimension, c) Contagion and d) Shannon diversity index .

Class level fragmentation

Class-level fragmentation analysis showed that the four honeybee habitat classes (i.e. woody vegetation, croplands, grasslands and hedges and the other landscape classes in the six test sites vary in the amount and patterns of land cover as shown in the Fig. (2.9). The highest percentage of woody vegetation cover was found in Mumoni (79.9%), Kathiani (47.43%) and Kasanga (38.76%), indicating that Mumoni area has nearly 15 times more woody or natural vegetation than Nguni (5%).

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In addition, cropland was above 30% in every site except in Mumoni where it was lowest at 13.5%, whereas for the hedges class, all the sites displayed levels below 10%, with Mumoni having the lowest percentage (<1%), which corroborates with the lower proportions of croplands in the same area (Fig. 2.9a).

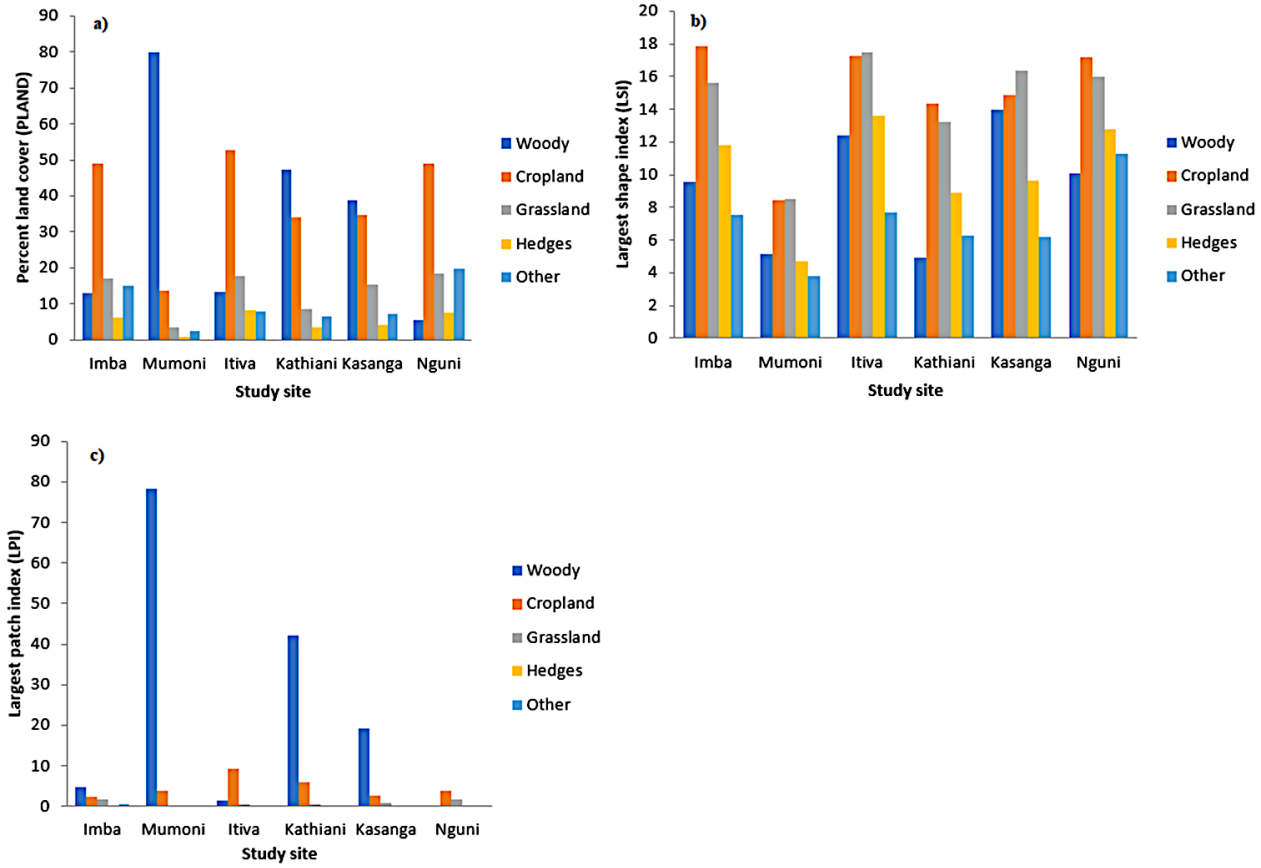

Figure 2.9: Class-level fragmentation indices for the honeybee habitats in the six test sites: a) percent land cover, b) largest patch index c) and largest shape index

Moreover, the highest LPI value was found in the woody vegetation class in Mumoni area (78.42), while the lowest value among the honeybee habitats was found in the hedges class within the Mumoni site (0.1054), which further corroborates the SI in Fig. (2.8a). This result clearly distinguishes the six landscapes in terms of landscape configuration (Fig. 2.9b) as well as indicating that Mumoni is the least heterogeneous of the six sites. Finally, the lowest LSI, Fig. (2.9c) values were found across all the honeybee habitats within the Mumoni area, except for the woody vegetation class, for which the Kathiani site had a slightly lower value (5.16 against 4.94, respectively). The rest of the classes had

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comparable LSI values across the remaining five sites. This again indicated that the least convoluted patch shapes were found in the Mumoni site for all the honeybee habitat classes.

2.4 Discussion

Mapping honeybee habitats is key to understanding the linkages between landscape characteristics and honeybee colony health and therefore fundamental in addressing issues related to honeybee population decline. Here, a multi-sensor approach using radar as well as optical data from the ESA Sentinel sensors, for mapping fine-scaled landscape structural elements, which contain honeybee habitats is described. Landscape-level and class-level fragmentation patterns in the study region is also reported on. It is observed that S2 data added a significantly improved overall accuracy to the bi-seasonal S1 data. Many studies have shown that the fusion of SAR with optical imagery improves classification accuracy (Balzter et al., 2015; Abdikan et al., 2016; Torbick et al., 2017), especially since optical imagery can add spectrally rich information in the visible-NIR, as well as in the RE spectrum. The inclusion of radar adds textural landscape information for time periods that are not detectable in optical imagery because of cloud cover (Hütt et al. 2016) . However, one study done in a semi-arid biome showed that SAR alone, even with the addition of texture parameters, was insufficient for land cover classification, even though SAR played a key role in increasing the interpretability of the resulting map. The authors argue that this may be due to the better vegetation discriminatory abilities of optical sensors over radar sensors especially in open and semi-arid landscapes (Braun and Hoschild, 2017).

Whereas the highest overall classification accuracies in this study were achieved with the fusion of S1 and S2 imagery, the dual-polarized and multi-temporal S1 image showed the highest PA for the under-represented honeybee habitats i.e. grassland and hedges (Table 2). The S1 classification scenario also had the highest UA for the cropland class. This demonstrates that S1 data could be used to map these specific honeybee habitats with acceptable levels of accuracy. However, the lower OA as well as moderate UA and PA for the woody vegetation from the S1 data may be explained by the similarity of the honeybee habitats which may not be so well discriminated by radar backscatter (Braun and Hoschild, 2017). The cropland class also had a lower PA under the S1 imagery compared to S2 and the fused S1-S2 imageries. It can therefore be recommended that the vegetation and cropland classes could be mapped using the S2 optical data, while S1 could be used to map the underrepresented honeybee habitats which are the grasslands and hedges (Fig.2.10). Fig. (10) shows a quasi-fused map composed of both S1 (hedges and grasslands) and S2 (woody vegetation and cropland).

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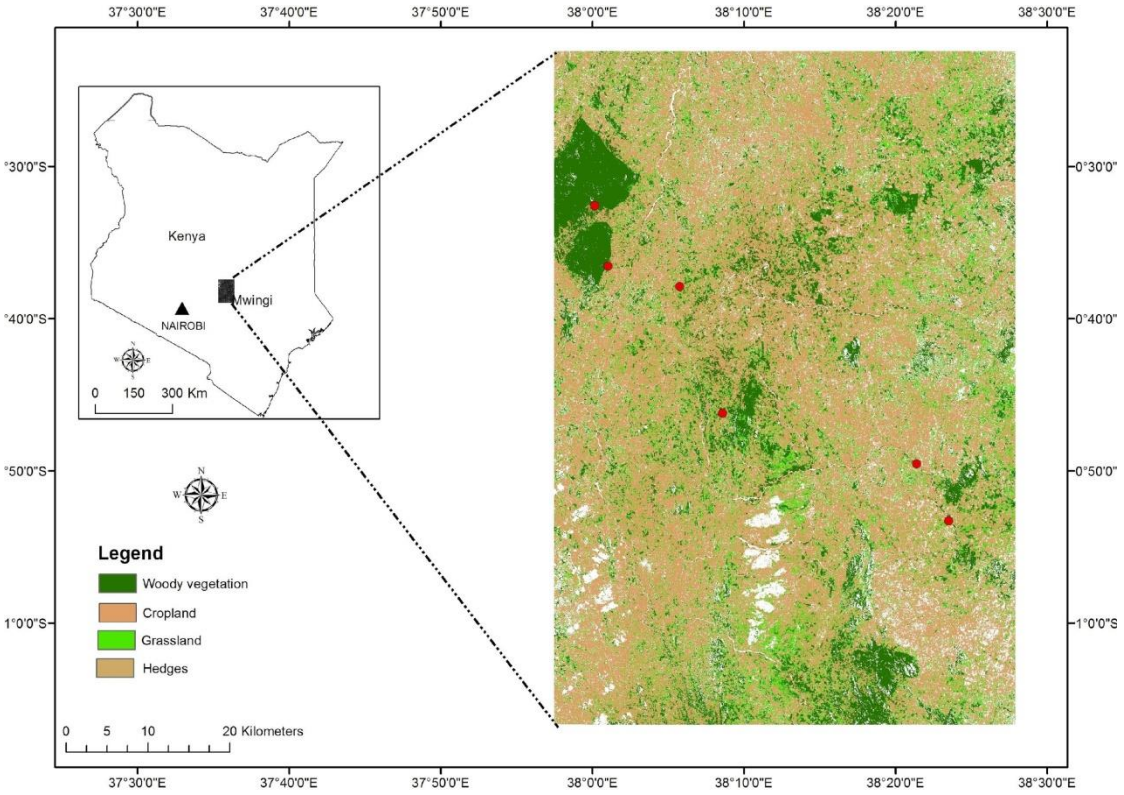

Figure 2.10: A quasi-fused map of honeybee habitats where grassland and hedges were mapped using Sentinel-1A (S1) and woody vegetation and cropland were mapped using Sentinel-2A (S2)

The intra-class variability among these LULC features could thus be larger than the inter-class variability between them, as frequently happens in heterogeneous landscapes and which therefore affects discrimination of these features (Ghimire et al., 2010). Interestingly, the fused S1-S2 data had low PAs for the grasslands and hedges classes, despite having a higher OA than any other data combination in this study. This may be explained by the structural similarity of these land cover classes especially in this heterogeneous landscape in Kenya whereby most hedges are made up of a mixture of woody vegetation and croplands as well as grasses.

A possible reason for the low PA achieved for the grasslands class by all the data combinations used in this study, is the lumping together of the various grasses into one grasslands class, whereas grasses are known to have various C3-C4 compositions which have large spectral variability (Adjorlolo et al., 2012; Foody & Dash, 2007). A more in-depth study aimed at differentiating these grasses would probably yield better accuracies for the grasslands mapping.

The importance of the SWIR and the newly available RE bands within the S2 sensor has been demonstrated in this study, given the high importance score for these bands that was derived using

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the RF variable importance by-product. The RE bands are particularly important due to their unique ability to distinguish between natural vegetation and cropland areas (Schuster et al., 2012).

The predicted fragmentation indices indicate varying fragmentation patterns evident at the spatial domains. Landscape-level indices demonstrate differences in patch size, shape and configuration, whereby the two relatively new indices by Jaeger (2000), the splitting index and the contagion index, show clear differences in both the patch sizes and connectivity of the study sites. The class level indices also showed differences in the test sites for each land cover class considered as important honeybee habitats. The percent land cover for woody vegetation is highest in the Mumoni site at approximately 80% and lowest in Nguni at < 10%. This indicated greater availability of natural honeybee habitats in Mumoni rather than Nguni. Again, cropland is highest in Nguni, Itiva and Imba at approximately 50% which may indicate the presence of seasonal forage for the honeybees, especially since honeybees forage on crop flowers in the absence of natural habitats (Corbet, 1991). As expected, because of their usage as fencing material, hedges are most abundant in areas also having the highest spatial occurrence of the cropland class. Consequently, depending on the species, this may also be a source of forage for the honeybees while simultaneously providing connectivity in fragmented landscapes (Hannon & Sisk, 2009). Regarding the LPI, (indicating the percentage of total landscape area characterized by the largest patch), Mumoni had the largest LPI under the woody vegetation class at around 78 as well as the lowest LPI under the hedges class (<1). This could be explained by the fact that Mumoni has the highest amount of natural areas and few croplands thus fewer hedges. The shape indices represented by the LSI showed consistently low values for Mumoni, which translates to simpler and less convoluted shapes in this area. This indicates least fragmentation in the area compared to the other sites. Given that fragmentation is known to negatively affect habitat quality for pollinators (Ritten et al., 2017; Rands, 2014; Rathcke et al., 2018), this index will be useful in the remote sensing of honeybee and other pollinator's habitat quality. It must however be emphasized that the outcome of this mapping exercise represents potential foraging resources for honeybees and not actual resources. Remote sensing methods as used in this study have certain limitations particularly with regard to spatial and temporal resolutions which may be unable to capture fine-scaled flowering which would represent actual foraging resources for the honeybees. Much higher spatial and spectral resolution would be required to achieve this as was achieved in Landmann et al. (2015). However, this method involved costly airborne hyperspectral sensors which may be unsustainable in these regions.

In summary, all the analysed landscape and class-level fragmentation parameters have implications for honeybee dispersal and accessibility to resources since foraging activities will vary in differently

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structured landscapes (Steffan-Dewenter & Kuhn, 2003a). Landscape fragmentation could be usefully employed for optimal placement of honeybee apiaries within this landscape in Kenya, similar to commercial farmers in the United States who purposively select apiary locations in order to ensure abundant forage for the colonies throughout the year (Otto et al., 2016).

2.5 Conclusions

Mapping of honeybee habitats in a semi-arid and heterogeneous landscape in Kenya was carried out using the image combinations from both S1 and S2 and results compared. The results showed that RF with fused S1 SAR and S2 optical bands gave the highest overall classification accuracy at 86.4% with a kappa of 0.83. However, the dual polarized and bi-temporal S1 image showed higher PA for grasslands and hedges which are the under-represented but important honeybee habitats and high UA for croplands. This is despite having a lower classification accuracy of 76%. This study demonstrates that in cases where optical data may not be available, as may be the case due to excessive cloud cover, SAR data can be effectively used to map honeybee habitats with appreciable accuracies.

SAR interferometric coherence methods consisting of 6-day pairs consisting of S1A and S1B are recommended for better mapping and differentiation of grasslands from woody vegetation acquisitions. The availability of these data pairs for the study region in the foreseen future should enable higher accuracies for mapping honeybee habitats.

Overall, this study demonstrates that the derived fragmentation indices can successfully encapsulate the variation in honeybee habitat quality at specific sites in a semi-arid landscape. These indices will form the basis for linking landscape quality with the honeybee colony strength and other measures of performance, which in turn could be used to assess the effect of the landscape characteristics on honeybee colonies across various seasons.

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3 CHAPTER THREE: FRAGMENTED LANDSCAPES AFFECT HONEYBEE COLONY STRENGTH AT DIVERSE SPATIAL SCALES IN AGROECOLOGICAL LANDSCAPES IN KENYA

This chapter is based on:

Pamela Ochungo., Ruan Veldtman., Elfatih M. Abdel-Rahman, Eliud Muli and Tobias Landmann, (2019). Landscape fragmentation and honeybee colony strength in agroecological landscapes in eastern Kenya. *Proceedings of Entomological Society of America (ESA) 2019*.

Presented at **Entomology 2019**, November 18th 2019, St Loius, Missouri, USA.

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Abstract

Landscape fragmentation and habitat loss at multiple scales directly affect species abundance, diversity, as well as their productivity. There is a paucity of information about the effect of the surrounding landscape structure and diversity on honeybee colony strength in Africa. The present study presents new insights into the relationship between landscape metrics such as patch size, shape, connectivity, composition and configuration and honeybee (*Apis mellifera*) colony strength characteristics in a typical highly fragmented African agroecological region in Kenya. Remote sensing-based landscape variables were linked to in situ determined honeybee colony strength variables using a unique data integration approach. The research was done within six sites of varying degrees of land degradation (LD), during the period from 2017 to 2018. Landscape structure was first mapped using medium resolution bi-temporal Sentinel-1 and Sentinel-2 satellite imagery with an optimized random forest mapping algorithm. The influence of the surrounding landscape matrix was then constrained to two buffer distances, i.e. 1 km representing the local foraging scale and 2.5 km representing the wider foraging scale around each investigated apiary and for each of the six sites. Using the landscape structure map, landscape and class fragmentation metrics were derived for each of the apiary buffer zones. The results of zero inflated negative binomial regression with mixed effects showed that lower complexity of patch geometries represented by Fractal Dimension (FD) and reduced proportions of croplands were most influential at local foraging scales (1 km) from the apiary, while higher proportions of woody vegetation and hedges resulted in higher colony strength at longer distances from the apiary (2.5 km). Honeybees in moderately degraded landscapes demonstrated the most consistently strong colonies throughout the study period. The results demonstrated that honeybee colony strength is influenced by landscape fragmentation at diverse spatial scales in African agroecological landscapes. Efforts geared towards improvement of beekeepers' livelihoods through higher hive productivity should consider landscape fragmentation characteristics at various distances from apiaries. Moreover, beekeeping efforts should be targeted at moderately degraded and heterogeneous landscapes, which avail forage from diverse land cover types.

Keywords: Landscape Fragmentation, honeybees, zero inflated negative binomial regression, Kenya

3.1 Introduction

Pervasive anthropogenic activities globally have resulted in habitat loss and consequently fragmentation of the natural landscape (Defries et al., 2004; Foley et al., 2005; Morris, 2010). Habitat

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fragmentation which is the division of the landscape into smaller and increasingly isolated fragments (Fischer & Lindenmayer, 2006) is mainly caused by agricultural intensification and human settlement. Consequently, these landscape fragments produce isolated habitat segments which modify the ecological interactions between the isolated segments (Jaeger, 2000). Such habitat modifications often hinder fundamental ecosystem functions leading to reduction of global biodiversity (Ewers & Didham, 2006; Haddad et al., 2015). For instance, forest fragmentation from human activities have been shown to modify plant species composition, subsequently adversely influencing carbon sequestration and water production characteristics (Edwards et al., 2014; Putz et a., 2014). Furthermore, fragmentation lessens animal and plant mobility across landscapes consequently interfering with their ability to forage, migrate, breed, and disperse (Fischer & Lindenmayer, 2006). Moreover, fragmented patches are smaller, with greater edge effects, therefore support smaller species populations and affect their overall persistence (Dobson et al., 2006; Harper et al., 2005).

Habitat fragmentation has specifically been shown to reduce the abundance and diversity of native insect pollinators, for example butterflies (Rodrigues et al., 1993) and bee assemblages (Aizen & Feinsinger, 1994). Further, pollinator richness as well as visitation rates to crops was shown to decline exponentially decline as distance to natural habitat increased (Ricketts et al., 2008), while pollinator diversity was shown to be threatened mainly by habitat loss (Brown & Paxton, 2009). Habitat fragmentation has also resulted in reduced genetic diversity among bee populations (Kremen et al., 2007). Potts et al. (2010a) described general negative effects of habitat loss and fragmentation on wild pollinators although there was little evidence of any effect on managed honeybees.

It has been shown that fragmentation of landscapes can lead to nutritional deficiency and thus lowered survival rates of honeybees from a lack of flora in the habitat (Naug, 2009). Additionally, it has been established that honeybee colony productivity is correlated with the surrounding landscape composition, therefore influencing the wellbeing of honeybees (Donkersley et al., 2014; Sponsler & Johnson, 2015). Moreover, honeybee colonies located near natural/semi-natural landscapes have higher hive productivity and survival rates (Brosi, 2009; Sande et al., 2009; Smart et al., 2016). In some instances, however, the surrounding landscapes have not displayed any strong effect on honeybee colony strength (Vaudo et al., 2012). Further study of the effects of landscape on honeybee colony performance is therefore required.

In Africa, the livelihoods of a significant proportion of the rural population is dependent on beekeeping as an income generating activity, mainly from sales of honey (Bradbear, 2009). Moreover, the honeybee (*Apis mellifera*) provides vital pollination services, which are crucial for improved food

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security in the region as well as provision of essential nutritional and medicinal benefits (Macharia, et al., 2007). Additionally, in Western Kenya, honeybees together with other pollinators are estimated to contribute US$3.2 million in ecosystem services to numerous crops in the region (Kasina et al., 2009). Populations of wild honeybee swarms are regularly trapped into hives to establish 'domesticated' honeybee stocks in the region (Dietemann et al., 2009) and beekeepers typically only interfere with the colonies during honey harvesting (Carroll, 2006). Given the 'wild' nature of honeybees in Kenya, it follows then that they will be greatly affected by habitat fragmentation especially with regard to their plant food sources (Macharia et al., 2007). This poses a tangible threat to the honeybees particularly because human population growth is increasing in Africa faster than any other place in the world (Cohen, 2003), subsequently resulting in increased habitat degradation and fragmentation. Likewise, beekeepers in the region are aware that small honeybee colonies result in low productivity and such colonies are discarded. This demonstrates that honeybee colony strength variables can be associated with productivity (Muli et al., 2014). However, there is a paucity of empirical studies that specifically address the association between landscape fragmentation and honeybees colony strength in Africa, unlike in European and North American countries where several studies exist (Aizen & Feinsinger, 1994; Brosi et al., 2008).

In this chapter, the effects of landscape fragmentation at both the landscape and class level were investigated on honeybee colony strength parameters in a semi-arid agroecological landscape in eastern Kenya, an area characterized by variable landscape degradation levels. Specifically, landscape fragmentation metrics that were derived from a comprehensive landcover mapping of honeybee habitats at the study site using medium resolution fused Sentinel-1 (S1) and Sentinel-2 (S2) datasets were utilized (Ochungo et al., 2019 and Chapter 2 of this thesis). The present study is unique since it links remote sensing-based landscape variables to in situ determined honeybee colony strength variables using a novel data integration approach. It was hypothesized that honeybee colonies situated in landscapes with a greater proportion of natural and semi-natural landscapes would exhibit higher colony strength than colonies located in landscapes with very little natural and semi-natural landscapes, due to greater availability of pollen and nectar providing plant species in such areas. The specific objectives were to (1) assess the influence of landscape fragmentation metrics on honeybee colony strength parameters and productivity and (2) to identify landscape fragmentation metrics that were strongly associated with honeybee colony strength and productivity across the study sites. This study will ultimately assist in identifying the optimum placement of honeybee colonies for maximal honeybee productivity. Furthermore, the study has broader implications for other pollinators since

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they can be envisaged to be influenced by the landscape fragmentation variables in a comparable manner.

3.2 Methods

3.2.1 Study area and study sites

The study was carried out in Mwingi sub-county within Kitui County in the south eastern part of Kenya (Figure 3.1). Mwingi area is an important honeybee keeping area in the country, and its beekeepers have a long association of cooperation with research institutions. It exhibits a semi-arid climatic pattern with average annual rainfall amounts ~ 700 mm. Temperatures typically range from ~ 15°C during the cold season to ~ 30°C during the hot months. The study area is made up of variable and heterogeneous landscape types, from highly vegetated zones in the north western region to degraded and sparsely vegetated drier areas towards the south east. The study area is predominantly an agroecological mosaic, consisting of maize and sorghum as the main crops (Landmann et al., 2015), which flower mainly in January, While the natural woodlands, chiefly *Acacia* spp., flower from February to April (Nagarajan et al., 2007), mainly driven by the short rainy period from November to December.

Six study sites were selected across various 'land degradation severity' gradients. These sites were predefined from field observations and consisted of the following: 1) the 'least-degraded': sites with plenty of natural vegetation i.e. higher proportions of woody vegetation, grasslands and hedges compared to croplands (Mumoni and Kathiani 2) 'moderately-degraded': sites consisting of mixed natural and cropland areas i.e. proportions of woody vegetation, grasslands and hedges occupied almost equal share of landscape as proportion of croplands (Kasanga and Itiva Nzou and 3) 'highly-degraded' sites with scant natural vegetation i.e. proportion of croplands was greater than proportion of woody vegetation, grasslands and croplands (Nguni and Imba) , and each were at least > 3 km from each other (Figure 3.1 and Table 3.1).

Ten 10-frame-hives were then placed in each of the six study areas (apiaries) and swarming was let to occur naturally in the field, as is typical in Africa. A multi-seasonal data collection was thereafter carried out.

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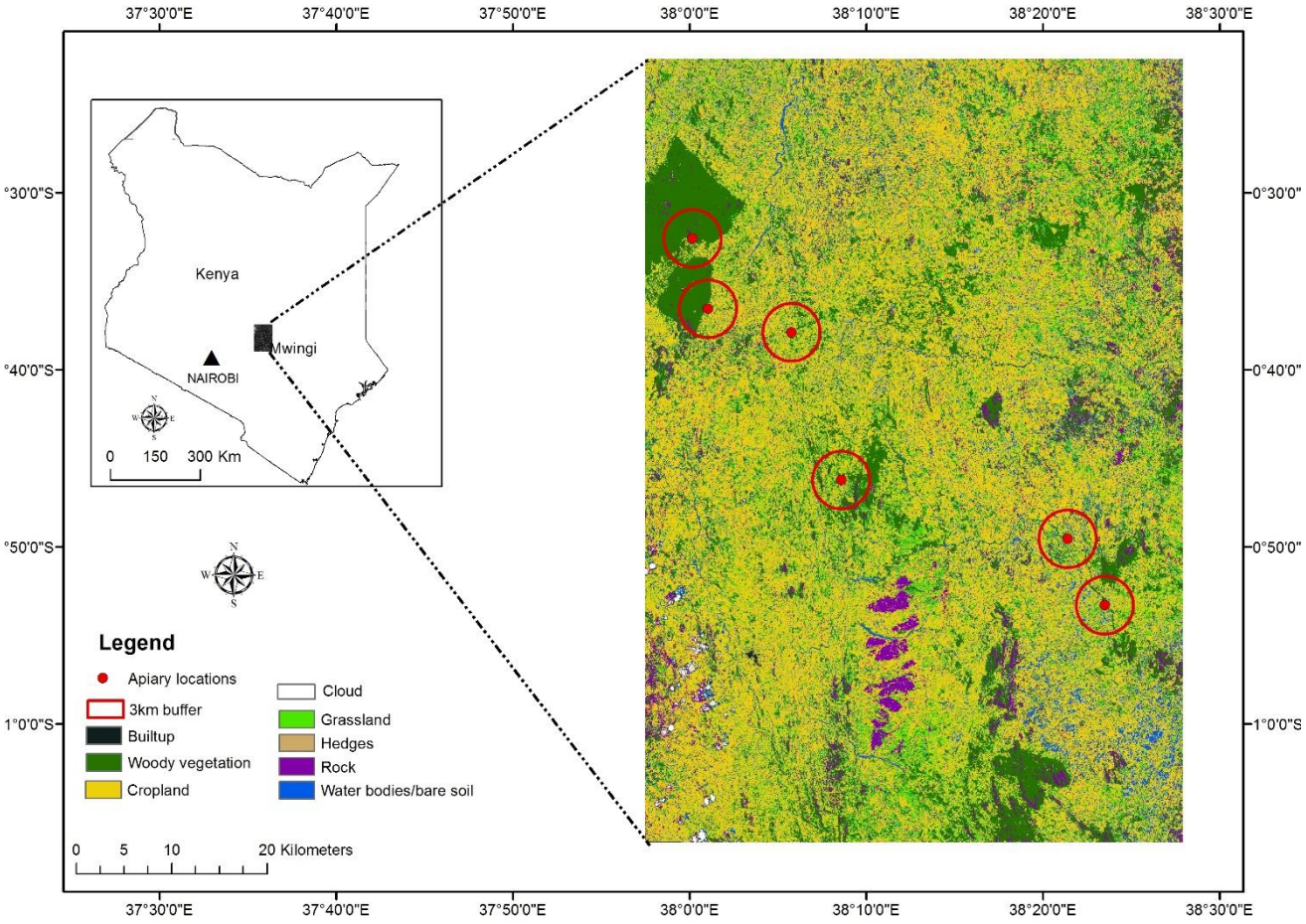

Figure 3.1: Location of the study region in Kenya (left) with the hives located in each of the six study areas, marked by red dots. A classified landcover map (S1-S2 fused data) of the study site is shown. Buffer zones from 500 m to 3 km were generated around the sites but for clarity, only the 3 km buffer zones are displayed here as red circles. (Source: Ochungo et al. (2019) and Chapter 2 of this thesis).

Table 3.1: Landscape characteristics of the experimental apiaries in Mwingi study area. Landscape composition comprising of proportions of woody vegetation, grasslands, hedges, and croplands for each apiary site is calculated within a 3-km buffer zone

Name of apiary	Latitude (East)	Longitude (South)	Percentage of woody vegetation	Percentage of grassland	Percentage of hedges	Percentage of croplands
Nguni	38.3561	0.82171	8.52	16.09	6.94	46.69
Imba	38.39139	0.887838	10.76	16.14	3.8	49.37
Itiva	38.09649	0.631461	18.61	16.72	11.04	45.43
Kasanga	38.14273	0.770265	31.13	15.72	4.09	43.71
Kathiani	38.01603	0.610229	41.64	9.46	5.05	39.43
Mumoni	38.00261	0.54305	76.97	1.58	0	19.24

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3.2.2 Honeybee colony strength measurements

Standard Langstroth hives were used for this study. Each of the hives were labelled randomly from 1 to 10 in each apiary and subsequently the frames in the hives labelled 1 to 10 with each side of the frame labelled A or B. 60 hives were initially setup for this study, i.e. 10 hives per site. However, throughout the study period, only 30 hives (i.e. colonies) spread across the 6 sites were inspected and sampled which were the only ones that occupied by natural swarm as observed during the first field data collection. Visual estimates from two observers were used, as this method is less disruptive compared to using empirical measurements such as weight of the honeybees (Delaplane et al., 2013), with one of the observers also recording the hive parameters. All the data measurements were conducted during the early hours of the day to control for the foraging activities of honeybees, which might affect the observations, especially of the adult honeybee population. Each of the occupied hives was lightly smoked, opened and frames containing combs were sequentially removed and examined. The estimated percentage coverage of each frame side by the target resource (adult population, sealed and open brood, eggs, honey and pollen) was visually done.

Honeybee colony strength was estimated following Delaplane et al. (2013) and Imdorf and Gerig (2001) Liebefeld protocol. When using this method, the type of hive and frame determines the approximation of these metrics. Table 3.2 shows the guiding values used for estimating the various comb types.

Table 3.2: Surface area of common frame types and estimated honeybee density when frame is completely occupied by worker honeybees, and worker cells density (Delaplane et al., 2013; Imdorf and Gerig, 2001)

Comb type	Surface per side of brood comb cm^2	Number of bees per occupied side of brood comb	Bees/cm^2	Worker cells/cm^2
Swiss	930	1200	1.29	4
Dadant	1130	1400	1.24	4
German normal size	720	900	1.25	4
Langstroth	880	1100	1.25	4

Parameters for the Langstroth hive were adopted (Table 3.2), and estimates of the African honeybee body size used following Buco et al. (1987), whereby the African honeybee is approximately 3%

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smaller than the African honeybees in South America (1.75 bees/cm^2). A value of 1.8025 honeybees/cm^2 was therefore logically used as the approximated size of the African honeybee. Further, 12 different combs from the six study sites were physically sampled and manually counted the number of cells in a 2 cm x 2 cm size comb area, to come up with the number of cells in a 1 cm x 1 cm comb area for each comb. The mean value of this exercise was 4.8 cells per 1 cm^2 of comb for this study area. These values were then used to convert the proportions of honey, brood, pollen and eggs on each side of comb into count values of these parameters.

Primary measures of colony strength i.e. adult population and brood (including eggs) and secondary measures consisting amount of stored pollen and honey were systematically collected in each hived colony over the entire study period (i.e. May 2017 to November 2018), deliberately selected to match different seasons in the region. The 30 hives were each inspected 5 times over a sampling period of 5 climatic seasons, i.e. 2 rainy (May and November) and 3 dry (January, February and June).

3.2.3 Landscape characteristics measurements

Remote sensing-based landscape metrics were computed by analysing habitat fragmentation at a maximum radius of 3 km around each georeferenced apiary, using concentric circles around the middle point of the apiaries. This radius was selected based on estimated honeybees foraging distance which is on average within 3 km from an apiary (Hepburn & Radloff, 1998; Roubik, 1989). These metrics can be used for estimating landscape composition and configuration, shape, heterogeneity, and connectedness and subsequently assessing their impact on honeybee colony strength. None of the apiaries were less than 3 km from each other.

In order to generate the landscape fragmentation indices, a honeybee habitat map was generated from a fused bi-temporal sentinel-1 and a single season sentinel-2 dataset (ESA, 2017), which had an overall accuracy (OA) of 86% (Ochungo et al., 2019 and Chapter 2 of this thesis), (Figure 1). Fragmentation indices were thereafter generated from the fused map at various spatial scales ranging from 0.5 km to 3 km (Table 3). Selection of these metrics was done based on their relevance to insects (Hunter, 2002). Besides, an index which was called ‘fractional cover of semi-natural vegetation to croplands (FNC)’ was derived as an additional fragmentation index since honeybees have shown improved performance with increased proximity to semi-natural areas (Patrício-Roberto & Campos, 2014; Sande et al., 2009). The FNC index essentially calculates the proportion of semi-natural vegetation compared to croplands in each of the study sites. A lower FNC indicates a lower proportion of semi-natural vegetation in a site, while a higher FNC indicates a greater proportion of semi-natural vegetation in a site. Furthermore, to quantify landscape heterogeneity, the Splitting Index (SI) (Jaeger,

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2000) was used. This index measures the number of equal-sized patches of a particular class, needed to produce a desired degree of landscape division (Jaeger, 2000). The Shannon diversity index (SHDI) which is a measure of the number of landscape elements together with their proportional changes was also computed. This index considers the abundance of the types of landscapes or landscape heterogeneity. The selection of SHDI was made on the basis of Morris et al. (2014) who demonstrated that simpler indices like SHDI were slightly preferable when detecting effects of land use on diversity. When comparing two or more landscapes, those with lower SHDI values are typically more homogeneous than those with higher SHDI values. Further, the contagion index (CONTAG) was selected to measure landscape connectivity, while the fractal dimension index (FD) represented complexity of patch geometry. To quantify class level fragmentation, the percentage of landscape (PLAND) measured the proportional abundance for each of the patch types across the landscape, whilst the landscape shape index (LSI) was selected to measure shape complexity at the class level. Finally, the landscape patch index (LPI) was used to quantify the percentage of total landscape area characterized by the largest patch (Mcgarigal, 2014)

Table 3.3: Class and landscape fragmentation indices used in this study (Mcgarigal, 2014)

	Index type	**Fragstat index**	**Description**
Class			
	Landscape composition	Percentage of landscape (PLAND)	The proportional abundance for each of (PLAND) the patch types across the landscape
	Landscape configuration	Largest patch index (LPI)	An index used to quantify the percentage of total landscape area characterized by the largest patch
	Landscape shape	Landscape shape index (LSI)	An index used to reflect the complexity of the landscape patches; a greater value indicates more complexity
Landscape			
	Landscape composition	Splitting index (SI)	Number of equal-sized patches of a specific class which is needed to produce a desired degree of landscape division

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Landscape shape	Fractal dimension (FD)	Measures the degree of shape complexity
Landscape composition	Shannon diversity index (SHDI)	Measures the number of landscape elements as well as their proportional changes. Also, the abundance of landscape types.
Landscape connectivity	Contagion (CONTAG)	A measure of the degree of adjacency of classes within a map
Landscape composition	Fractional cover of natural to croplands (FNC)	An index which measures the proportion of semi-natural vegetation to croplands

3.2.4 Data analysis

Assessing multicollinearity and variable selection optimization

All statistical analyses were implemented using R version 3.5.3 (R core team, 2019). Two methods were utilized to assess multicollinearity in the fragmentation variables. The 'findCorrelation' and the Recursive Feature Elimination (RFE) bootstrapping methods (Yan & Zhang, 2015a) were used concurrently to account for collinearity and disregard those indices which were highly correlated. As part of the 'findCorrelation' method, firstly, a Spearman's rank-order correlation test was conducted at each buffer distance scale between all the fragmentation parameters (Table 3.3) to determine whether there were relationships among them with the intention of eliminating multicollinearity. There was a total of 96 landscape fragmentation metrics at both the class and landscape-level at buffer distances and most of these metrics were found to be highly correlated. Therefore, the 'findCorrelation' function in the caret package in R (Kuhn, 2019) was used to exclude highly correlated variables using the mean absolute error score. The caret package has demonstrated robustness in the selection of predictor variables (Kyalo et al., 2018; Mudereri et al., 2020). A threshold correlation coefficient of $|r| > 0.75$ was set to indicate variable collinearity that would influence the outcome of this model (Dormann et al., 2013). Fragmentation parameters which were highly correlated were then eliminated. Further, the RFE bootstrapping method was also used for automatic feature selection at every buffer distance. The RFE is a feature-ranking algorithm which performs optimization algorithms to achieve an optimal subset of variables (Pullanagari et al., 2018). Variables are ranked according to their importance after a process whereby every variable in the out-of-bag data is randomly rearranged. A ten-fold cross validation is used to achieve optimization of the

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variable selection, after which the root mean squared error (RMSE) values are evaluated by the algorithm and those with large values are eliminated. This process is recursively exercised until the best variables with the lowest RMSE are identified (Pullanagari et al., 2018). The caret package in R (Kuhn, 2019) was once again used to conduct the RFE on the landscape variables.

Landscape fragmentation variables which were selected by both the 'findCorrelation' and the RFE functions were chosen for use in the regression analysis. In instances where there was no commonality between the selections from the two feature elimination functions, the RFE selection was used. Further, two radii were selected for the analysis, i.e. the 1 km radius to represent typical honeybee foraging, and the 2.5 km to represent the larger landscape in which the apiaries were situated. The following variables were selected at the 1km radius: Fractal dimension (FD), Percentage of landscape under cropland (PLC), Landscape shape index for woody vegetation (LSW), Landscape patch index for cropland class (LPC) and fractional cover of natural to cropland (FNC). Further, the following variables were selected at the 2.5 km radius: Percentage of landscape under grassland (PLG), Percentage of landscape under woody vegetation (PLW), Largest patch index for hedges class (LPH), Percentage of land under hedges (PLH) and fractional cover of natural to cropland (FNC).

Linking landscape variables and honeybee colony strength metrics

The uncorrelated landscape fragmentation characteristics at the two selected radii (1km and 2.5km) were compared with the field-collected honeybee colony data (adult bee population, brood, honey, pollen, and eggs) at hive level. Zero-inflated negative binomial (ZINB) mixed models were used to analyse for each of the response variables. ZINB mixed models are normally used in cases dealing with count data which display over dispersion with a large proportion of zeros (Loeys et al., 2011; Sileshi, 2006). Further, the full distribution of the regression result is denoted by two separate sections, a first part displaying the probability of extra zeros (logit model) and a second part providing for the non- excess zeros and non-zero counts (negative binomial model) (Loeys et al, 2011; NCSS Statistical Software, 2014). ZINB data has demonstrated its usefulness in modelling ecological data which is frequently characterized by many zero values (Martin et al., 2005). Moreover, due to the hierarchical quality of the data collection, which involved repeated in situ data collections within each of the sites and colonies, mixed effects involving random and fixed effects were also applied, with colony nested within site as random effects. Mixed-effects models allow for the use of all the data, while avoiding the use of individual colonies as pseudo-replicates (Chaves, 2010; Crawley, 2002). All the data analyses were carried out within the R statistical programming language (R Development Core Team, 2019) using the glmmTMB package (Magnusson et al., 2020). Additionally, to simplify

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the regression model, backward stepwise variable elimination was carried out on the predictor variables using AIC values to remove variables whose p-value was non-significant in the regression outcome (NCSS Statistical Software, 2014). Residuals for each response variable were then plotted using r package DHARMa (Hartig, 2020)

3.3 Results

3.3.1 Honeybee colony strength measurements

Data distributions of the honeybee colony strength response variables displayed large proportions of zero counts. Appendix D, Figure D1 shows the distributions of adult honeybee populations and number of cells of honey only since the distributions for the rest of the colony strength parameters exhibit a similar pattern. Further, honeybee colony strength characteristics summed across the five data collection periods showed that the two study sites in the moderately degraded areas (Kasanga and Itiva) displayed the highest colony strength parameters throughout the data collection period whereas the two study sites in the highly degraded areas (Nguni and Imba) showed the lowest values (Appendix D, Figure D2).

3.3.2 Landscape fragmentation variables versus honeybee colony strength

Scaled residuals for each of the response variables at the 1 km and 2.5 km scales indicated that overall deviations from the expected distribution, including tests for accurate distribution (KS test), dispersion and outliers were not significant, therefore indicating good model fits, as shown in Appendix D, Figures D3 and D4, respectively.

Examination of the count component model coefficients and p-values (Table 3.4) at the 1km scale showed that fractal dimension (FD) was the most important variable since it was significant in both the count and zero components of the models. Lower FD values resulted in higher adult honeybee counts and cells of honey and conversely, higher FD values resulted in zero adult honeybee population counts, cells of honey and cells of pollen. Furthermore, higher landscape shape index of woody vegetation (LSW) resulted in higher adult honeybee counts and higher number of cells of honey, whereas lower proportion of cropland (PLC) and lower fractional cover of natural to croplands (FNC) resulted in higher adult honeybee population. At the 2.5km scale, the proportion of woody vegetation (PLW) was the most important variable since it was significant in both the count and zero components of the models for most of the honeybee colony strength variables. A higher PLW resulted in higher adult honeybee populations, higher number of cells of brood, honey, and pollen, whereas a lower PLW resulted in zero counts of adult honeybee populations, cells of brood, honey, pollen and eggs. Additionally, lower proportions of grasslands (PLG) and hedges (PLH) resulted in zero adult

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honeybee populations, cells of brood, honey, pollen and eggs, while larger patch size index of hedges (LPH) resulted in zero values for all the honeybee colony strength parameters (Table 3.4).

Table 3.4: ZINB model parameters of the response of population of all the honeybee colony strength parameters (n = 150) to landscape fragmentation predictors at 1 km and 2.5 km radii. Zero component results show how predictors affect the odds of observing excess zeros in adult honeybee populations while count component results show how predictors affect the population of adult honeybees. Only significant variables are shown.

		Zero component					**Count component**			
Scale	Parameter	Variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
1km	Adult worker bee population	FD	48.25	20.99	2.30	*	-22.08	10.09	-2.19	*
		PLC	0.03	0.33	0.10	.	-0.36	0.16	-2.31	*
		LSW	-0.64	0.34	-1.86	.	0.42	0.15	2.76	*
		FNC	0.51	2.77	0.18	.	-3.05	1.35	-2.26	*
	Cells of honey	LSW	-0.65	0.33	-1.93	.	0.27	0.13	2.11	*
		FD	48.70	20.09	2.42	*	-9.26	7.44	-1.25	.
	Cells of pollen	FD	44.67	18.94	2.36	*	-13.14	10.64	-1.24	.
2.5km	Adult worker bee population	PLG	-0.26	0.11	-2.34	*	0.08	0.05	1.66	.
		PLW	-0.15	0.05	-3.09	*	0.04	0.02	2.13	*
		LPH	0.30	0.11	2.63	*	-0.08	0.06	-1.42	.
		PLH	-1.24	0.41	-3.05	*	0.23	0.16	1.43	.
	Cells of brood	PLG	-0.34	0.12	-2.90	*	0.18	0.06	2.86	*
		PLW	-0.21	0.05	-3.76	*	0.07	0.03	2.36	*
		LPH	0.49	0.16	2.95	*	-0.05	0.10	-0.54	.
		PLH	-1.66	0.48	-3.49	*	0.27	0.27	1.01	.
	Cells of honey	PLG	-0.26	0.11	-2.34	*	0.09	0.08	1.22	.
		PLW	-0.16	0.05	-3.26	*	0.06	0.03	2.29	*
		LPH	0.21	0.12	1.80	.	-0.07	0.09	-0.75	.

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	PLH	-1.22	0.41	-2.95	*	0.35	0.24	1.49	.
Cells of pollen	PLW	-0.13	0.05	-2.90	*	0.09	0.03	3.19	*
	PLH	-1.03	0.38	-2.69	*	0.48	0.22	2.14	.
Cells of eggs	PLG	-0.27	0.13	-2.12	*	0.07	0.06	1.05	.
	PLW	-0.20	0.07	-2.96	*	0.05	0.04	1.41	.
	LPH	0.57	0.22	2.64	*	-0.21	0.12	-1.78	.
	PLH	-1.83	0.60	-3.04	*	0.46	0.32	1.43	.

Significance codes: <0.05 '*', > 0.05 '.'.

Individual tables for each of the honeybee colony strength parameters i.e. adult honeybee population, cells of brood, cells of honey, cells of pollen and cells of eggs are shown in Appendix D, Tables D1 to D5.

3.4 Discussion

The main objective of this study was to assess the effect of landscape fragmentation on the colony strength of honeybees, within a short foraging range of the apiary (1km) and within the larger landscape (2.5km) in a semi-arid region of Kenya. Overall, the negative effect of the fractal dimension variable for the count component of the model at the 1km scale indicates that patch geometries which were less complex had a positive effect on adult honeybee population, brood, honey and pollen. This is in agreement with Brosi (2009) who found that forest fragment shape was the most important landscape factor affecting euglossine bee's abundance and species richness. Moreover, Reynolds et al. (2007) demonstrated that honeybees search for the most optimal and efficient paths to return to their hives after foraging. Complex patch geometries would hypothetically lead to inefficient use of the honeybee's energy and consequently weaker adult workers who cannot forage effectively for pollen and nectar. Further, simpler patch shapes are also associated with lower landscape fragmentation which can be important for different ecological processes (Forman, 1995). Similarly, the positive effect of the fractal dimension variable on the probability of occurrence of zero values for nearly all the honeybee colony strength parameters agrees with the finding in this study, that complex shapes negatively affected the colonies.

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Further, the negative effect of the proportion of croplands variable in the count component of the model at the 1 km radius from the apiary on adult honeybee population is in agreement with findings by Clermont et al. (2015) who found that agricultural lands were associated with honeybee colony losses probably due to reduced foraging resources from semi-natural land covers. Moreover, a study by Vandame and Palacio (2010) found that colony losses were low in Brazil, possibly due to lower proportions of cropland within the total land area, and therefore availability of plentiful pollen supplies for honeybees. Likewise, Otto et al. (2016) and Vaudo et al. (2012) also demonstrated that croplands negatively affect honeybee colony strength.

Proportion of woody vegetation at the larger landscape radius (2.5 km) had a positive effect on all the honeybee colony strength parameters except eggs in the count component of the model. Moreover, in the zero component of the model, this variable had a negative relationship with all the honeybee colony strength parameters. It is thus clear that honeybee colonies that are found in landscapes with abundant woody vegetation will demonstrate greater colony strength. This finding was expected since woody vegetation provide foraging resources for the honeybees at different times of the year depending on their floral cycle (Potts et al., 2010b). Further, these findings corresponded with those of Arthur et al. (2010) who demonstrated the importance of woody vegetation for densities of feral honeybees although within a shorter distance of the apiary. Higher amounts of stored honey have also been linked to shorter distances to woody vegetation (Sande et al., 2009). Similarly, woody vegetation was shown to improve both the abundance and richness of both wild bees and domesticated honeybees as demonstrated in a study by Schrader et al. (2018), mainly due to the availability of floral resources in such areas. Likewise, Bertrand et al. (2019), demonstrated the importance of trees as sources of pollen for insect pollinators.

Interestingly, there was a strong positive effect of the proportion of hedges in the landscape at the 2.5 km scale on number of honeybee cells with stored pollen. In a study by Hannon & Sisk (2009) hedgerows were shown to support a diverse herbaceous flora which formed a key foraging habitat for bees. Similarly, Winfree et al. (2008) proposed that hedgerows should be included in farmlands because they have been shown to improve visitation to crops by pollinators which further strengthens the results of this study. Additionally, hedges have also demonstrated their necessity in facilitating pollinator movement between habitat fragments (Cranmer et al., 2012). Likewise, a lower proportion of hedges in the landscape increased the probability that honeybee hives would be unoccupied.

Furthermore, there was no effect of the proportion of grasslands variable in the count component of the model. However, in the zero component of the model, lower proportions of grasslands had a

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negative effect on all the colony strength parameters. This finding can be interpreted that lower proportions of grasslands in the landscape would increase the probability of zero values occurring in the colony strength variables. These results correspond with those of Simanonok et al. (2020) who found that grasslands supported pollen amounts and quality, which directly influence honeybee colony strength. Moreover, Otto et al. (2016b) emphasizes on the importance of grasslands for honeybee colonies. In addition, the fractional cover of natural over cropland (FNC) variable had a negative effect on the population of adult honeybees at the 1km scale in the count component of the model. While this was unexpected, it could point towards the need for diverse landscapes closer to the hive rather than homogeneous natural landscapes. Furthermore, in sub-tropical Africa, agroecological landscapes are typically heterogeneous, and these types of landscapes have been shown to enhance pollinator richness and abundance due to the landscape diversity (Aguirre-Gutiérrez et al., 2015; Steckel et al., 2014)

While it had been hypothesized that apiaries in the least degraded sites would have the strongest colonies, it was established that the apiaries in the moderately degraded sites had the most consistently strong colonies throughout the study period (Appendix D, Figure D2). This pattern is similar to the 'intermediate disturbance hypothesis' whereby pollinator species and abundance have been found to be higher in moderately disturbed landscapes compared to completely undisturbed habitats (Coulin et al., 2019; Hinners et al., 2012). Such areas are comprised of heterogeneous landscapes with different types of crops, and consequently, a diversity of weeds and grasses. These crops, weeds and grasses have been shown to provide honeybee forage during periods when the semi-natural woody areas are not flowering (Bretagnolle & Gaba, 2015; Odoux et al., 2012). Also, the abundance of weeds has been shown to enhance pollination services and consequently improved honey yields (Bretagnolle & Gaba, 2015). On the other hand, apiaries in the two least degraded sites experienced the most absconding, again contrary to the postulation of this study. During the periods when the honeybees had absconded in these areas; several (> 20) large African hive beetles (*Oplostomus fuligineus*) were found inside these empty hives and speculated that these pests could have caused absconding. These beetles have been reported to cause significant damage to colonies, by chewing on the comb, brood, honey and pollen (Oldroyd and Allsopp, 2017; Wambua et al., 2019). Further, a study by Makori et al. (2017) showed that honeybee pests occurred more in areas with higher proportion of natural vegetation, which is in agreement with the findings of this study. Such areas should therefore be targeted for pest control exercises if honeybee colonies are to have maximal productivity and strength.

The influence of spatial scale on the wellbeing of honeybees has also been demonstrated in this study. This finding is in agreement with Taki et al. (2010), who found that landscape factors at different

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spatial scales affected crop yields by both managed and wild pollinators. Further, Bhakti et al. (2018) examined the effect of several spatial scales on the occurrence of forest birds in a tropical landscape and established that measuring landscape variables at multiple scales can further help ensure that the probable significance of landscape factors for describing species characteristics are adequately captured at specific scales.

3.5 Conclusions

Simpler patch shapes closer to the hives are shown to be more favourable for stronger honeybee colonies as well as higher hive productivity. Further, lower proportions of croplands closer to the hive are also shown to be beneficial for honeybees' colony strength, emphasizing the importance of semi-natural vegetation for providing foraging resources. Moreover, at the larger foraging scale, higher proportions of semi-natural vegetation and hedges are shown to be advantageous for honeybee colony strength. Overall, honeybees located in moderately degraded landscapes had the most consistently strong colonies throughout the study period, implying that heterogeneous landscapes are the most suitable for honeybee keeping in the region. Additionally, it is observed that honeybees in the least degraded landscapes had unexpectedly high rates of absconding, and large hive beetles which were found in the hives could possibly be a reason for the honeybees' inclination to abscond.

While the number of study sites limits the generalizability of the results, this approach offers new insights into the relationship between landscape characteristics and honeybee colony strength. To better understand the implications of these results, future studies could build upon these results by increasing the number of study sites and possibly using higher spatial and temporal resolution remote sensing datasets. Further, based on these conclusions, beekeepers should consider optimal hive placement based on fragmentation characteristics of an area, for maximal productivity of their colonies.

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4 CHAPTER FOUR: POLLEN DIVERSITY AND NUTRITIONAL CONTENT IN DIFFERENTIALLY DEGRADED SEMI-ARID LANDSCAPES IN KENYA

This chapter is based on:

Pamela Ochungo, Ruan Veldtman, Rahab Kinyanjui, Elfatih M. Abdel-Rahman, Eliud Muli, Michael N. K. Muturi, and Tobias Landmann. (2019). Pollen diversity and nutritional content in differentially degraded semi-arid landscapes in Kenya. *Journal of Apicultural Research* (Under revision)

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Abstract

In Africa there is a dearth of information as to how plant species vary across differentially structured landscapes, and therefore the possible implications to honeybee colony strength. This research presents new insights into the diversity and richness of pollen collected by honeybees in six study sites of different degradation levels within a semi-arid landscape. Six apiaries were established in a study area in Kenya which had also been mapped using novel remote sensing methods and land cover characteristics extracted. Pollen in the form of bee bread was regularly collected in five data collection exercises, with three colonies in each of the six sites (i.e. apiaries) repeatedly sampled during the period from May 2017 to November 2018. Pollen identification and protein analysis were thereafter conducted. Out of 124 plant species identified, *Terminalia* spp., *Cleome* spp. and *Acacia* spp. were identified as the most abundant species overall. Moreover, species richness and diversity were highest in the two apiaries located in moderately degraded landscapes, while high plant species evenness was observed in the highly degraded landscapes as well as in one apiary located in the least degraded areas. Pollen protein content showed statistically significant differences across season rather than geographical location. This study demonstrated that landscape characteristics affect pollen diversity and richness. Consequently, this will help in augmenting the understanding of honeybees' forage resource usage and plant species preferences in agroecological landscapes with varying degrees of degradation.

Keywords: Pollen, honeybees, Kenya, diversity, landscapes

4.1 Introduction

Honeybees (*Apis mellifera*) provide valuable ecosystem services via pollination, consequently contributing immensely to crop production globally (Hung et al., 2018; Potts et al., 2010). This crucial ecosystem service occurs because the pollinators forage for and harvest the nectar and pollen which they need for their development (Di Pasquale et al., 2013). Pollen is the fundamental protein source for honeybees, additionally providing vitamins, lipids and minerals essential for honeybees development particularly the brood and queen (Brodschneider & Crailsheim, 2010; Danner et al., 2016). Principally, protein content in pollen has generally served as a measure of the quality of pollen (Roulston et al., 2000; Vaudo et al., 2015). Honeybees preserve their collected pollen in the form of 'bee bread' which is a blended mix of honey and worker bee glandular secretions (Anderson et al., 2014; Brodschneider & Crailsheim, 2010). This 'bee bread' is used by the nurse bees for feeding the growing bee brood and is essential for their development, principally due to the inherent protein

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content (Degrandi-Hoffman et al., 2010; Alaux et al., 2017; Keller et al., 2005). Subsequently honeybee health has been reported to be dependent on the abundance and diversity of pollen mainly for the brood (Rasmont et al., 2005; Somerville & Nicol, 2006) as well as nectar for the adult honeybees, which ensures a wide variety of nutrients for the honeybees (Di Pasquale et al., 2013).

However, shifts in landscape characteristics mainly due to increasing landscape fragmentation and subsequent habitat degradation, have altered how honeybees utilize the foraging landscape for nectar and pollen (Dolezal et al., 2016). Pollen diversity has been directly linked to landscape structure and composition (Matthias et al., 2015), as various plants tend to provide different quality of protein in various proportions (Seeley, 1995; Andrada & Tellería, 2005; Estevinho et al., 2012). For instance, pollen harvested from landscapes composed of mainly intensive farmlands were shown to have lower nutritional value than those collected from landscapes with floral diversity (Requier et al., 2015; Dolezal et al., 2016; Donkersley et al., 2014). Consequently, honeybees fed on pollen with lower nutritional status especially with regard to protein demonstrated higher vulnerability to pathogens (Di Pasquale et al., 2013), thereby affecting overall health of the bees and possibly contributing to the observed decline in honeybee populations (Vaudo, 2015). Likewise, the importance and contribution of pollen from croplands as part of honeybees nutrition, has also been demonstrated (Odoux et al., 2012). Moreover, early honeybee colony growth has been shown to be positively correlated with amounts of pollen from woody vegetation.

Additionally, landscape degradation and fragmentation have been shown to affect floral availability and diversity. For instance, reduced patch fragments sizes were shown to have fewer plant communities when evaluated against bigger fragments (Raghubanshi & Tripathi, 2009). Furthermore, the larger fragments were generally characterized with diverse and richer plant species (Raghubanshi & Tripathi, 2009). Conversely, it has also been demonstrated that species may thrive in fragmented landscapes which are composed of both semi-natural and man-made landscapes which provide varied resources during the different seasons of the year (Krauss et al., 2003; Mandelik et al., 2012). Previous studies on the linkage between landscape structure and pollen have indicated that landscape composition has an influence on the distances which honeybees travel to forage for pollen (Danner et al., 2014; Steffan-Dewenter & Kuhn, 2003) which is therefore likely to affect their health. Further, it has also been demonstrated that honeybees will most likely forage on particular plants based on their preferences and not necessarily proximity of the floral resources (Visscher et al., 1982; Olsen et al.,1979). Temporal variation in protein content has also been shown to occur considerably with increases in protein content seen during late spring season (Keller et al., 2005). Likewise, in this study region, colony growth closely follows the bimodal rainy season patterns (March–May is the long

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rains and October–December is the short rains), hence March–May and November are main honeybee colony reproductive seasons. November is the midpoint of the short rain season following a prolonged dry season (June – Mid October) (McMenamin et al., 2017).

To the best of my knowledge, there is no documented information in Kenya and most of Africa as to the linkage between landscape degradation levels and abundance and diversity of pollen. It is hypothesized that pollen diversity is highest in the least degraded areas due to presence of a wide variety of natural vegetation which provides pollen for the bees. This chapter therefore intends to investigate this knowledge gap, given the high rate of conversion of natural and semi-natural landscapes into croplands in the region (Nkonya et al., 2015). The effects of landscape degradation level on pollen diversity and protein content in six apiaries situated within three distinctly varying landscapes in study area in Kenya (as defined in Ochungo et al., 2019 and Chapter 2) were examined. The study area is a semi-arid agroecological landscape, typical of most rural landscapes in the country and several other African countries. The specific objectives of this study were to (i) establish the pollen sources for the honeybees at study sites of varying degree of landscape degradation, and (ii) to determine the protein content of the pollen at the same sites. Generally, the hypothesis was that pollen diversity and protein content would be higher in the least degraded landscapes.

4.2 Methods

4.2.1 Study area and landscape characteristics

Six experimental apiaries were established in Mwingi, a subcounty in the eastern region of Kenya (Figure 4.1). Mwingi is made up of largely heterogeneous landscapes, mainly consisting of farmlands interspersed with shrublands, woody vegetation and grasslands. Some sites of the subcounty have more natural vegetation than others that have been highly degraded mainly due to agricultural expansion (Fening et al., 2008). The six study sites were chosen based on landscape degradation severity gradients, defined within a 3 km radius as following: 1) if proportion of woody vegetation, grassland and hedges occupied the largest share of the landcover composition, compared with proportion of croplands, it was considered to have low degradation, 2) if the proportion of woody vegetation, grassland and hedges occupied an almost equal share of the landscape as the proportion of croplands, then it was considered moderately degraded, and 3) if the proportion of croplands was greater than the proportion of woody vegetation, grasslands and hedges, then it was considered highly degraded (Table 4.1 and Figure 4.2). The landscape composition data for the six study sites were extracted from fused remotely sensed data sets, combining 10-meter Sentinel-1 (S1) (radar) and 10-

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20 meter Sentinel-2 (S2) (optical) bi-temporal satellite imagery (ESA, 2017). Each site consisted of an apiary and each was located at least 3 km apart. Initially each apiary comprised 10 Langstroth hives, thus a total of 60 hives. However, throughout the study period, only 30 hives (i.e. colonies) inspected and sampled, which were the only ones that were occupied by natural swarms as observed during the first field data collection. The data collection was repeated five times during the two rainy (May and November) and three dry seasons (January, February, and June). Collection of flowering materials for pollen referencing were carried out within a 3 km buffer zone from each apiary, mimicking the average foraging distance for honeybees (Hepburn and Radloff 1998; Roubik, 1989). The major documented flowering plant species in Mwingi are *Acacia* spp., *Boscia* spp., *Grewia* spp., *Aspilia mozambensis, Cassia diambotia, Cassia semea*, *Euphobia* spp., *Terminalia brownii* and *Solonium incunum*, of which most of them flower after the rainy seasons in December-January and May (Abdel-Rahman et al., 2015)

Table 4.1: Landscape characteristics of the experimental apiaries in Mwingi study area. Landscape composition comprising of proportions of woody vegetation, grasslands, hedges, and croplands for each apiary site is calculated within a 3 km buffer zone.

Name of apiary	Latitude (East)	Longitude (South)	% woody vegetation	% grassland	% hedges	% croplands
Nguni	38.3561	0.82171	8.52	16.09	6.94	46.69
Imba	38.39139	0.887838	10.76	16.14	3.8	49.37
Itiva	38.09649	0.631461	18.61	16.72	11.04	45.43
Kasanga	38.14273	0.770265	31.13	15.72	4.09	43.71
Kathiani	38.01603	0.610229	41.64	9.46	5.05	39.43
Mumoni	38.00261	0.54305	76.97	1.58	0	19.24

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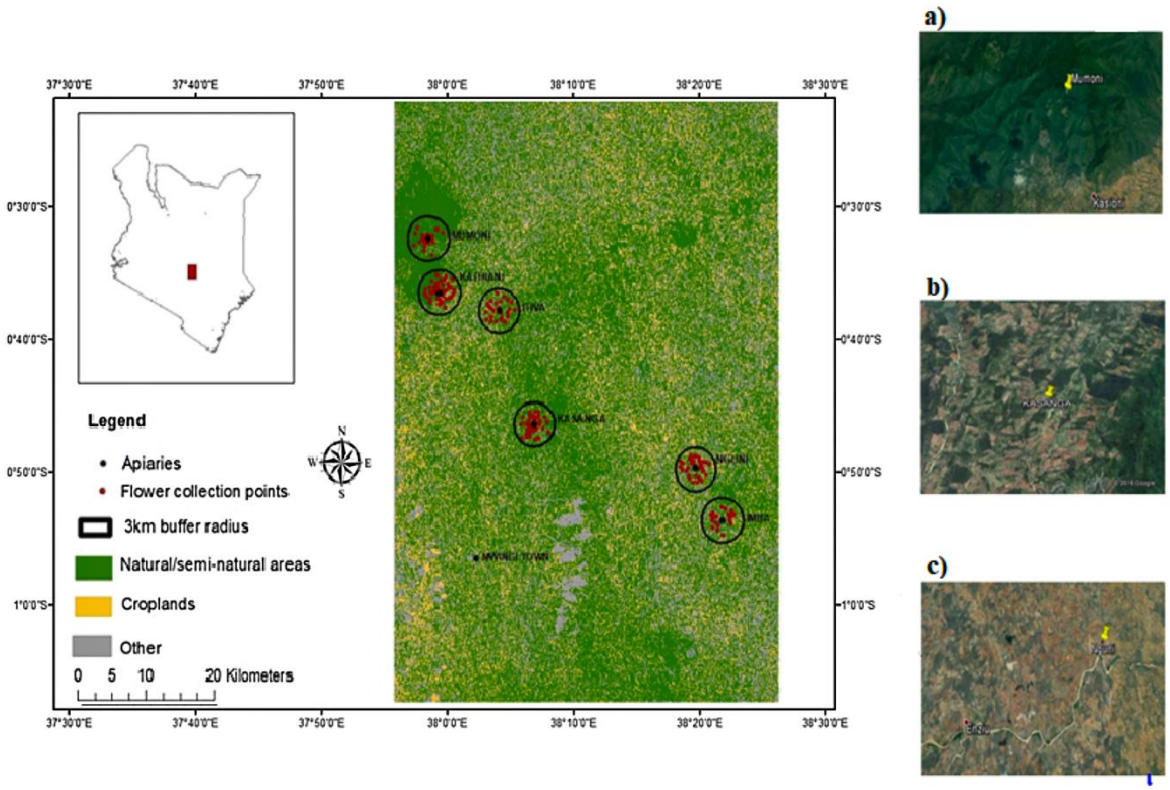

Figure 4.1: Location of the study area in Kenya (left) and classified map showing natural/semi-natural (woody vegetation, grasslands, and hedges) and cropland areas (predicted using the S1-S2 fused data) of the study area. The red points are the locations where flowers were collected for reference plant species throughout the study period. The images on the righthand side indicate the general degree of landscape degradation for the six sites i.e. a) high proportion of woody vegetation (low degradation), b) moderate proportion of woody vegetation (moderate degradation), and c) low proportion of woody vegetation (high degradation), from top to bottom, respectively (Google maps, 2017).

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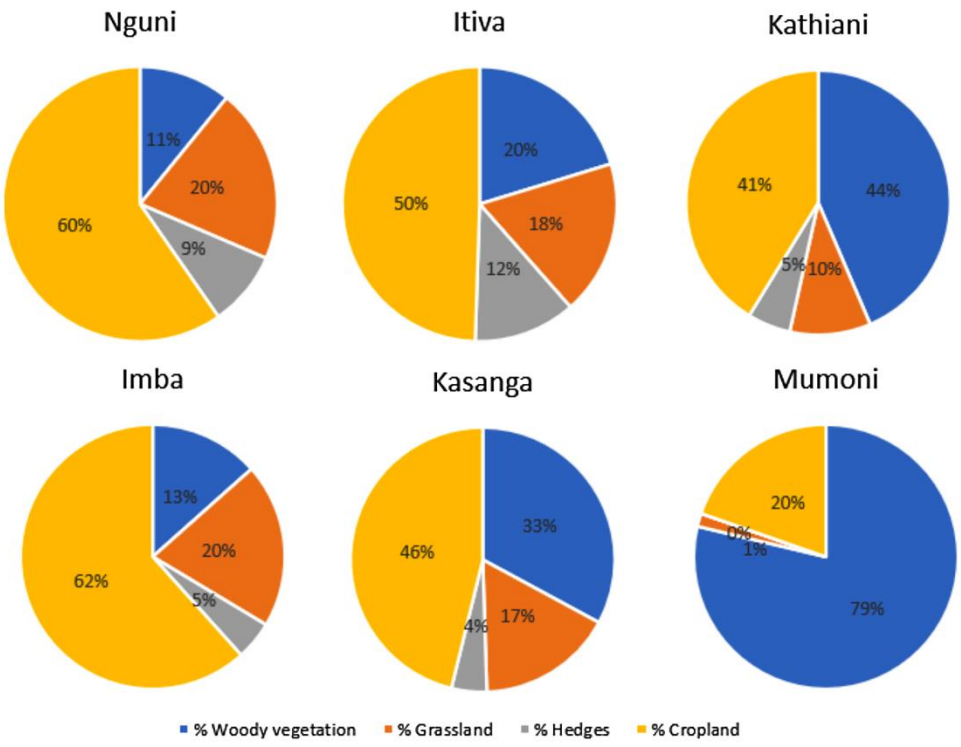

Figure 4.2: Proportions of woody vegetation, hedges, grasslands, and croplands in the six study sites.

4.2.2 Pollen Collection

The study was conducted between May 2017 and November 2018 during which a total of five data collection periods were carried out. The five data collection periods spanned the wet and dry seasons of the year i.e. May and November are typically wet seasons, while January, February and June are dry seasons. Experimental colonies were obtained from natural swarms and housed in Standard 10-frame Langstroth hives. Pollen in the form of bee bread was collected from three hives per apiary at each data collection period, except in cases when fewer than three hives had honeybee bread or where the colonies had absconded. All available bee bread was collected in such cases, and it was also recorded if no pollen was available for collection at specific sites. Pollen freshness was based on lack of fermenting odour (Menezes et al., 2013; Hoover & Ovinge, 2018; Vollet-Neto et al., 2017). In total, 35 separate bee bread samples (11 in low, 14 in moderate, and 10 in high landscape degradation classes) consisting of mixed pollen were collected. The bee bread was stored in falcon tubes at -20^{o}C while in the field, and subsequently at -80^{o}C in the laboratory for long term storage and analysis.

4.2.3 Protocol for processing pollen samples for taxonomic identification

Distilled water (2 ml) was added to each bee bread sample, vortexed and then 1 ml of each sample was used for pollen identification. An acetolysis method (Erdtman, 1969) where 9 parts of acetic

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anhydride and one part of concentrated sulfuric acid were thoroughly mixed to form the acetolysis mixture was used. Approximately 10 ml of the mixture was added to each vial containing the pollen sample to remove excine to allow accurate morphological identification of the pollen. Each sample was then washed using dH20, centrifuged and the supernatant decanted to obtain the pollen residue. Lastly, the pollen samples were washed with glycerin of 50% concentration, centrifuged and decanted. Then 100% glycerin was added to the samples for storage and mounting purposes.

Pollen residue (20 µl) was mounted on the microscopic slides, then a cover slip was placed over it carefully to ensure no bubbles were trapped. Prepared slides were studied to determine pollen diversity to a genus level and tallied the identified pollen grains. For slides rich in pollen, counting stopped after counting >800 grains. For the slides with less pollen grains, a second slide was prepared, and complete slides were studied. Identification and counting of pollen was done using the standard pollen atlases (Bonnefille, 1971; Gosling et al., 2013; Riollet & Bonnefille, 1976) and consultation of the modern pollen reference collection available at the National Museums of Kenya (NMK), Palynology and paleobotany laboratory. Any unidentifiable pollen was subsequently labelled as 'unknown'. Thereafter, pareto charts were generated for all sites combined.

4.2.4 Pollen protein extraction and determination test

Using a pestle and mortar, each bee bread sample was crushed, and a sample of 0.025 g was taken as per de Sá-Otero et al. (2009a) suggestions and then transferred into a microcentrifuge tube. Protein was extracted from the samples by applying the method used by de Sá-Otero et al., (2009) with slight modifications. Onto each of the samples, 4 ml of Tris-EDTA buffer was added and vortexed to ensure uniform mixing. The sample mixture was spun for 20 mins at 10 000 rpm and afterwards, the supernatant was collected in 0.1 ml aliquots. Further, 5 ml of Bradford reagent was added, leaving the setup for 2 minutes at room temperature (Bradford, 1976). The samples were measured using a spectrophotometer against an absorbance of 595 nm. Tris-EDTA buffer of 0.1µl was used as blank. 50 µl 150 µl , 200 µl , 250 µl and 400 µl dilutions of Bovine Serum Albumin (BSA) served as the standards for generating a calibration curve.

The absorbance values of the standard BSA were plotted against the protein concentrations, and the concentration of the protein samples was determined by linear regression model. This allowed the crude protein values of the pollen to be quantified using the standard curve generated (expressed in g/100g).

4.2.5 Pollen diversity and crude protein data analysis

Alpha diversity

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All data and statistical analyses as well as figure generation were implemented using the 'vegan' package (Oksanen, 2017) in R version 3.5.3 (R core team, 2019) and PAST version 4.0.1 tool (Hammer et al., 2001). Pollen composition at species level and family level were first calculated for each of the six sites and number of taxa computed. Thereafter, species accumulation curves (sample and individual rarefaction, Mao Tau's) were generated to determine the species richness of the pollen as a function of the quantity of samples (sampling effort). Further, rank abundance dominance (RAD) models were produced to compare species evenness in all the sites. These plots were used to indicate the logarithmic species abundances versus plant species rank order for the study sites (Gardener, 2014). For each site, five RAD models were utilized in the 'vegan' package viz., Broken stick, Lognormal, Mandelbrot, Preemption and Zipf models (Appendix E, Table E1). Each of these models takes the logarithmic abundance and rank of abundance as input data, and uses various parameters to fit models (Gardener, 2014). For each site, the model with the lowest Akaike Information Criterion (AIC) was selected and the curve was plotted (Appendix E, Table E2). Furthermore, in order to compare alpha-diversity at the six sites, diversity ordering using the Renyi index was used and the output plotted (Oksanen, 2017). Since the data were not normally distributed (Shapiro-Wilk, p-value = 0.00986, w = 0.95368), the Kruskal-Wallis rank sum test at 95% confidence level were then applied to analyse differences in diversity among the sites and post hoc contrasts were conducted using pairwise Wilcoxon's rank sum test for multiple comparisons.

Beta diversity

To evaluate beta diversity of pollen across the study sites, non-metric dimensional scaling (NMDS) technique was adopted, whereby after several iterations, k=4 dimensions produced the lowest stress value (< 0.2) (Taguchi & Oono, 2005). The Bray-Curtis distance matrix was used to create a dissimilarity matrix, while NMDS ordination was used for visualization. A permutational multivariate analysis of variance (PERMANOVA) was used to test the ability of geographical site to explain variation in the NMDS plot (Oksanen, 2017). A Shephard's diagram was produced to demonstrate the goodness of fit for each pollen sample. Subsequently, a pairwise similarity percentage (SIMPER) test was carried out to assess which pollen taxa were responsible for the observed differences among the pollen samples (Clarke, 1993). The SIMPER test was carried out between four pairs of sites, which demonstrated the largest separation on the NMDS plot. This analyses was implemented using the 'vegan' package (Oksanen, 2017) in R version 3.5.3 (R core team, 2019).

Protein data analysis

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For the analysis of crude protein in pollen, Kruskal-Wallis rank sum test at 95% confidence level was carried out to analyse the differences in crude protein concentration in pollen across the six study sites and across the months (seasons) of the year. The 'Devtools' and 'dplyr' packages in R were used for this exercise.

4.3 Results

4.3.1 Pollen identification

A total of 124 plant species belonging to 57 families were identified across all 6 sites. Pareto charts showing their combined distribution across the six sites are shown in Figure 4.3. For the combined distribution, a threshold was determined based on the pareto chart, whereby those species whose numbers did not contribute to the cumulative 100% were excluded. Further, Figure 4.4 shows plant composition at the family level in a stacked chart for each of the six sites in order of their degradation levels.

Species accumulation curves showed that overall species richness as a function of the sampling effort was satisfactory, based on the shape of the curve asymptote. However, individual rarefaction curves indicated that some sites were more exhaustively sampled than others (Figure 4.5).

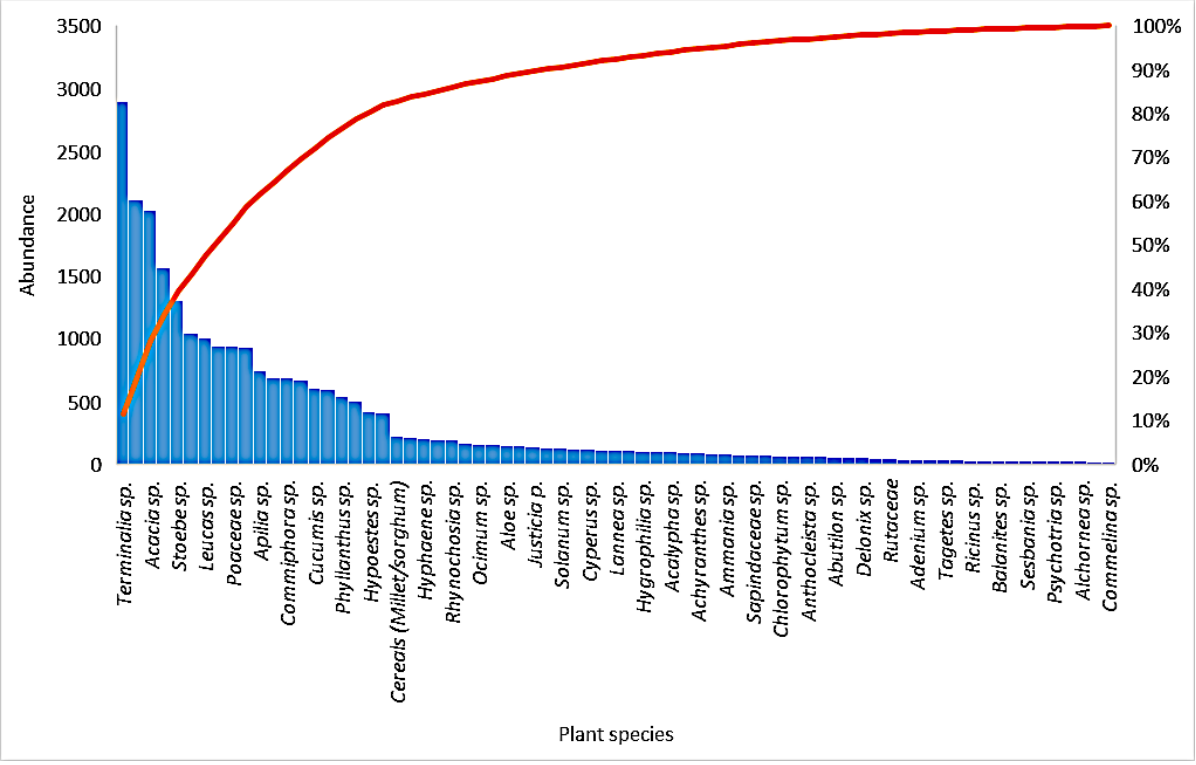

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Figure 4.3: Plant species abundance and cumulative values in all the six study sites. The *Terminalia* spp., *Cleome* spp. *and Acacia* spp., were the most abundant species overall.

The most abundant plant families were the Capparaceae (15.9%), Combretaceae (14.1%) and Asteraceae (13.6%), all with individual pollen counts > 3,000 across all the sites (Appendix B).

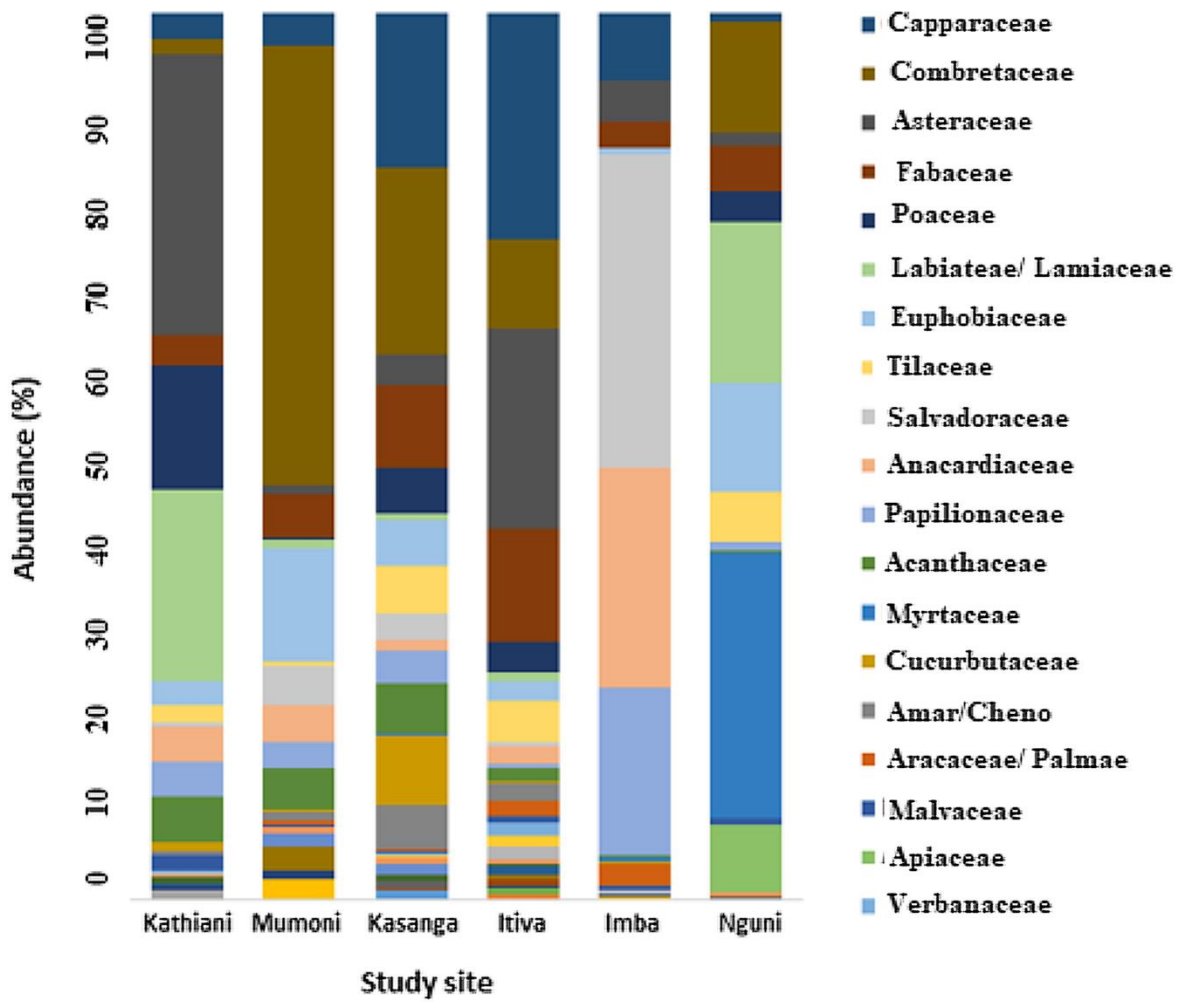

Figure 4.4: Plant composition at family level according to the bee bread diversity scores in the six sites presented in the following order: Least degraded (Kathiani, Mumoni), moderately degraded (Kasanga, Itiva) and highly degraded (Imba, Nguni).

4.3.2 Pollen diversity

Alpha diversity

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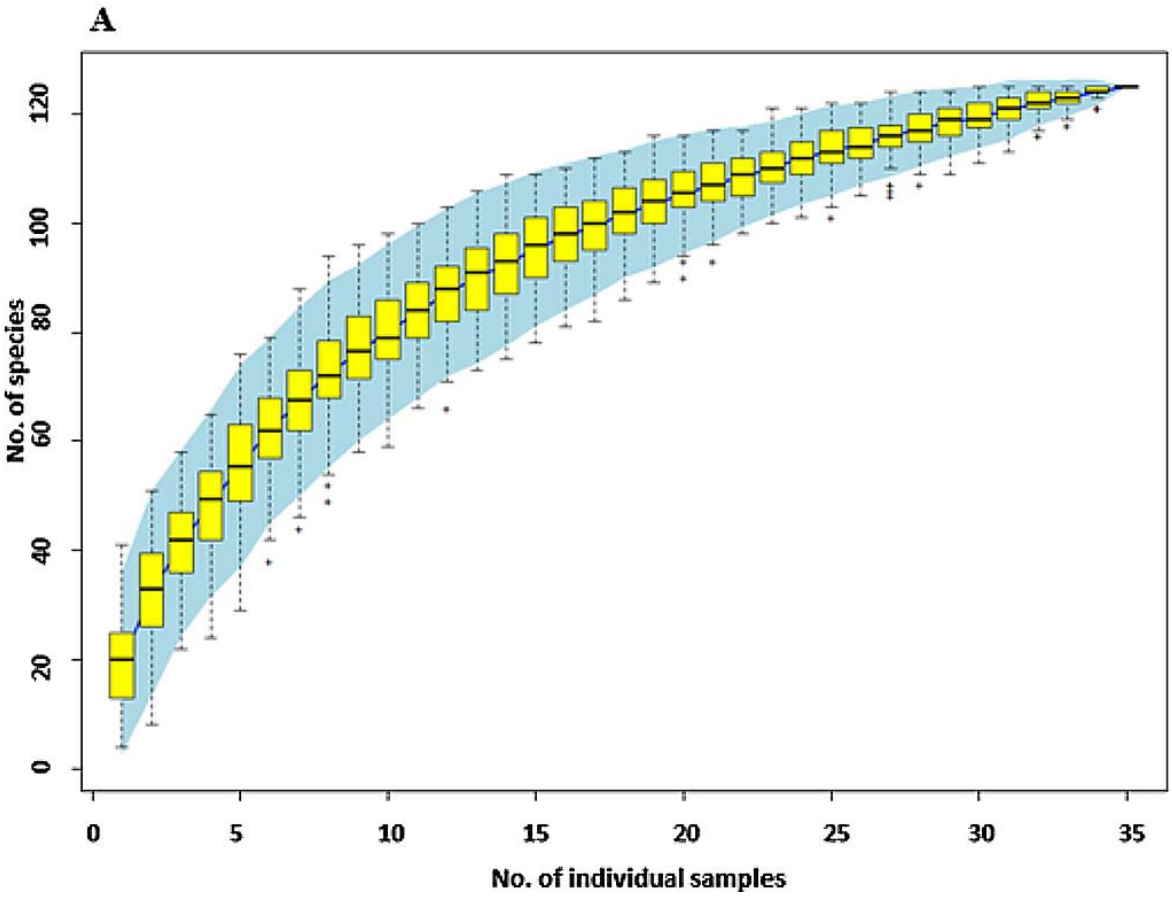
Figure 4.6 shows the results of the selected RAD models with the lowest AIC for each site. The steepest gradients are seen in the high degradation sites (panels 5 and 6), showing lower species evenness in these sites.

Additionally, Renyi diversities for the six sites showed lowest diversity values for the highly degraded sites (mean = 1.87) and highest diversity values for the moderately degraded sites (mean = 2.61) (Figure 4.7). Average diversity of the least degraded sites was 2.05, averaged for the α-values (total richness, Shannon-Wiener, Simpson-Yule and Berger-Parker).

Further, a statistically significant difference was observed in diversity across the sites (p-value = 0.01157; Kruskal-Wallis Chi-squared = 14.732) using Renyi diversity metrics (Figure 4.8)



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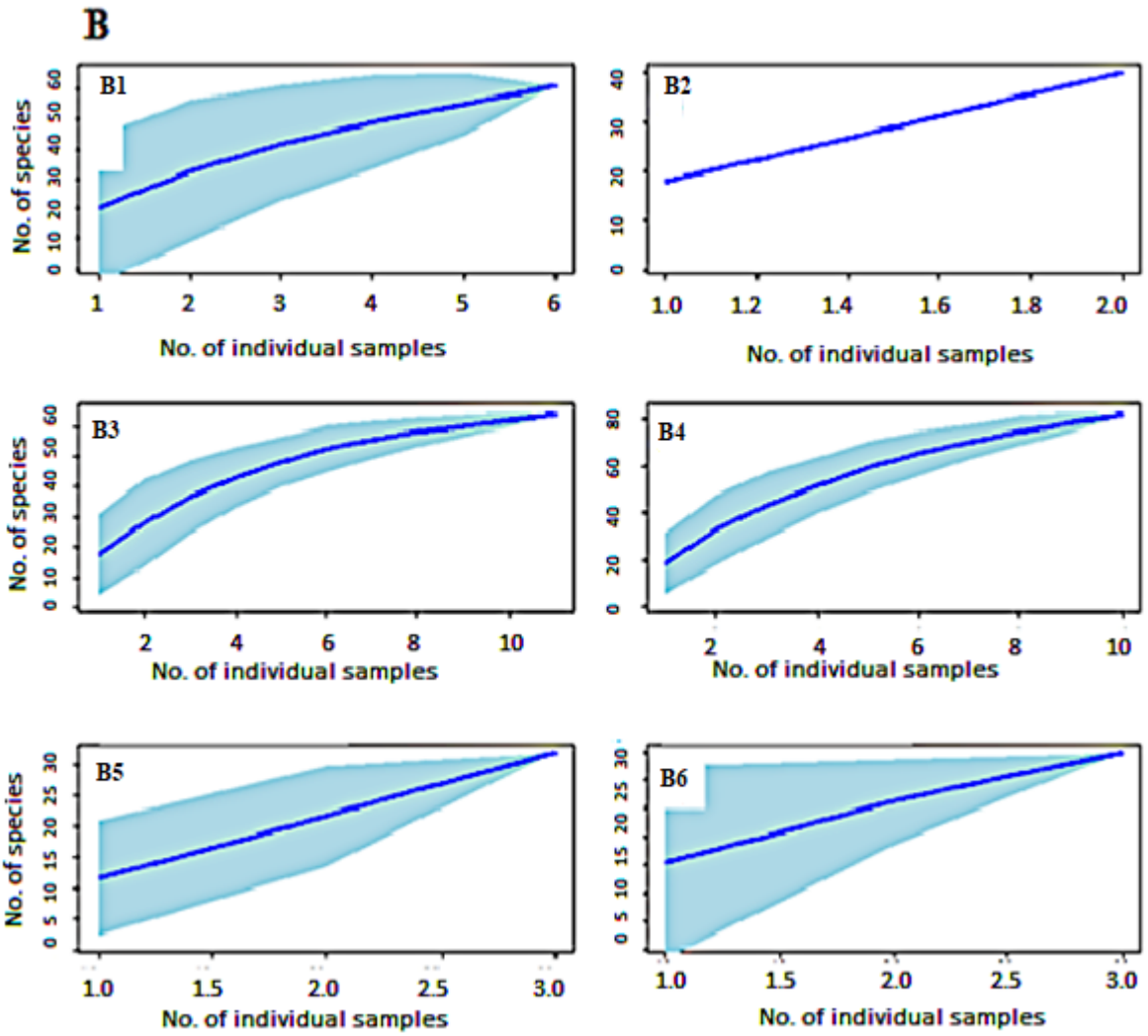

Figure 4.5: Species accumulation curve (Mao Tau's sample rarefaction) showing the total number of pollen samples versus the sampling effort that was required to observe them. The asymptote of the curves demonstrates that overall, the pollen samples were not sufficiently sampled. B: Individual rarefaction curves showing the total number of plant species (y-axis) versus the number of samples that were acquired at individual sites. The panels are arranged in the following order: B1 = Kathiani, B2 = Mumoni, B3 = Kasanga, B4 = Itiva, B5 = Imba, B6 = Nguni. Light blue shading around the blue line represents bootstrapped 95% confidence intervals.

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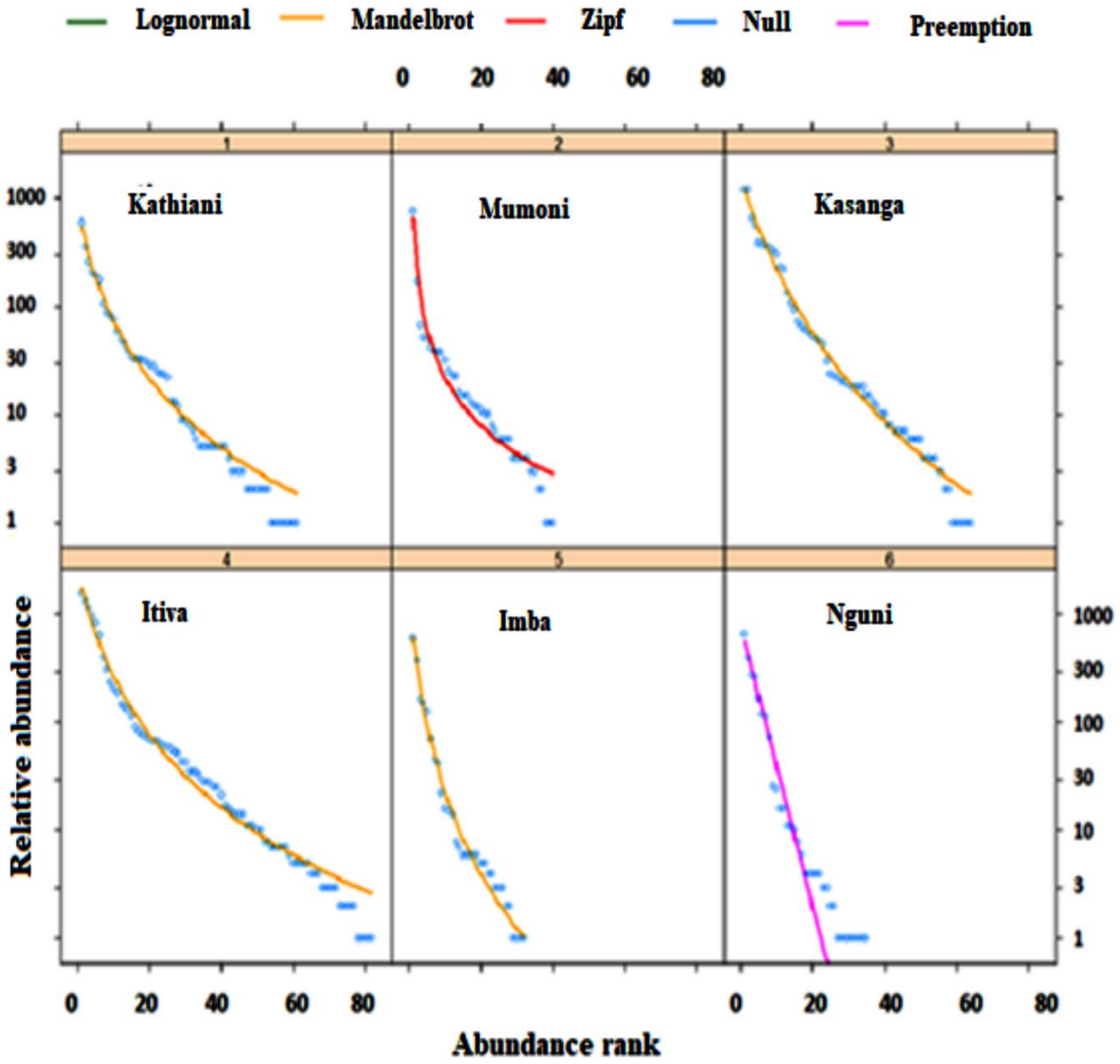

Figure 4.6: RAD models for the six study sites, falling within various land degradation levels. Individual panels show the RAD model with the lowest AIC. A steeper gradient demonstrates low evenness while a shallow gradient demonstrates high evenness which indicates that the abundances of the different species (both high and low ranking) are comparable to each other.

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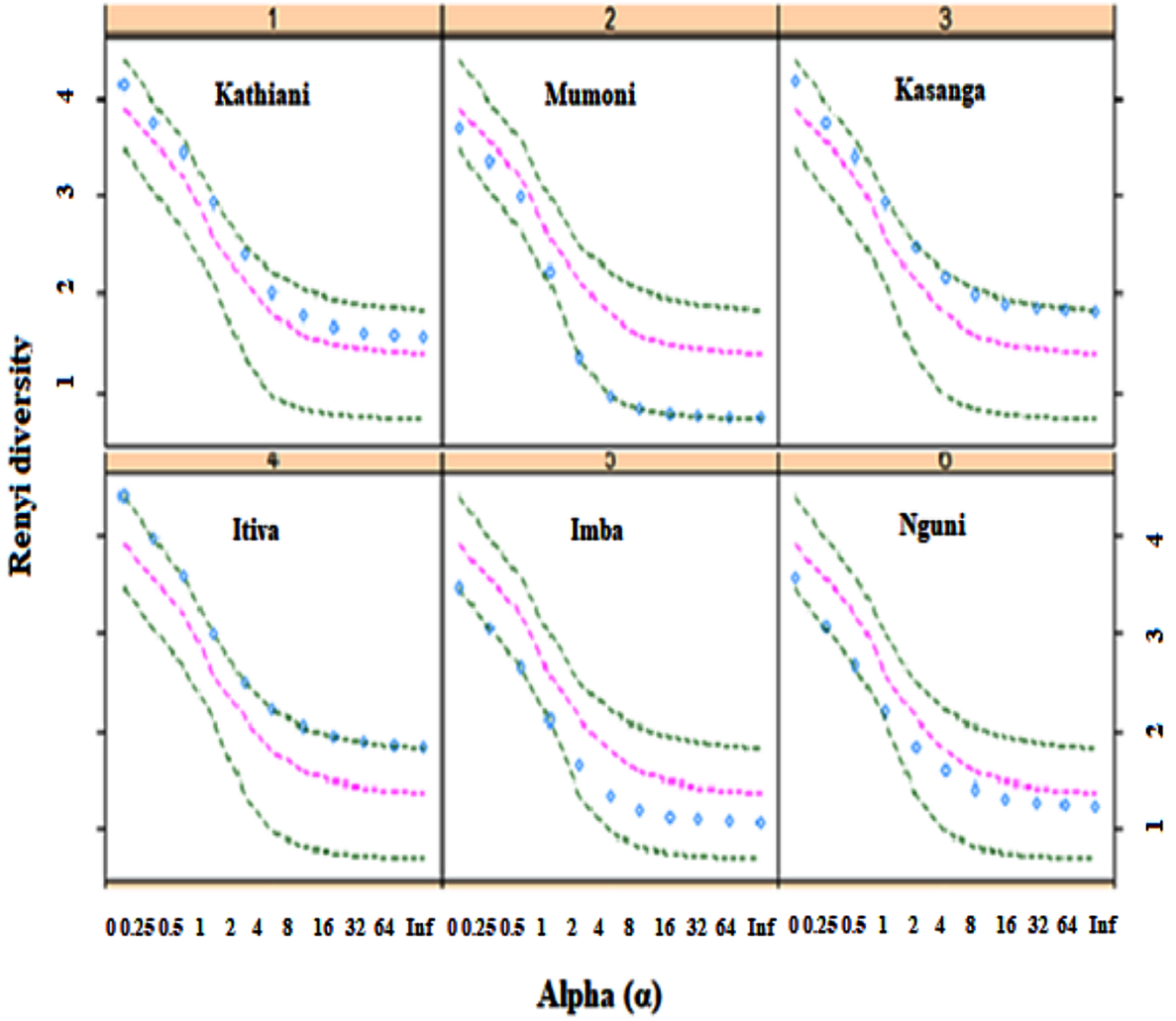

Figure 4.7: Renyi diversities in the six study sites. The blue dots in each panel display the diversity values for sites, whereas the dashed lines show the median value (pink) and extreme values (green). The y-axis shows differences in plant species diversity between each site whereas for the x-axis, the Renyi index approximates total species richness for $\alpha = 0$, Shannon-Weiner index for $\alpha = 1$, the inverse Simpson-Yule index for $\alpha = 2$ and 1/Berger-Parker index for $\alpha = Inf$ (p-value = 0.01157, Kruskal-Wallis Chi-squared = 14.732, df = 5).

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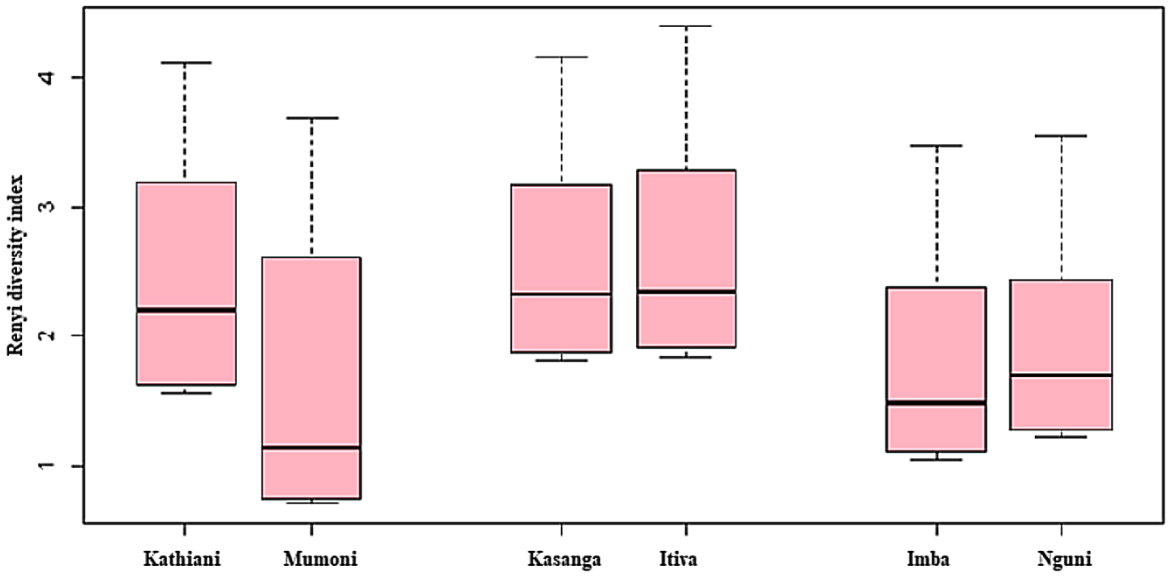

Figure 4.8: A comparison of the Renyi diversity indices for pollen samples from all six sites. The boxplots show the distribution of α values across all samples. Pairwise comparisons are shown in Appendix E, Table E3.

Beta diversity

Pollen composition between the six sites displayed overlaps and the overall dissimilarity was not significant as shown by the results from PERMANOVA: F-value = 1.19; p-value = 0.0722; Stress = 0.1239001, non-metric R2 = 0.985; Linear R2 = 0.843; k = 4 (Figure 4.9). However, pairwise results from PERMANOVA showed significant dissimilarities between Itiva and Nguni only, with p-value = 0.0421. PERMANOVA, F-value = 1.19; p-value = 0.0722; Stress = 0.1239001, non-metric R2 = 0.985; Linear R2 = 0.843; k = 4. A Shepherd's diagram, with correlation statistics demonstrating the goodness of fit of the pollen samples from the NMDS analysis is shown in Appendix E, Figure E1.

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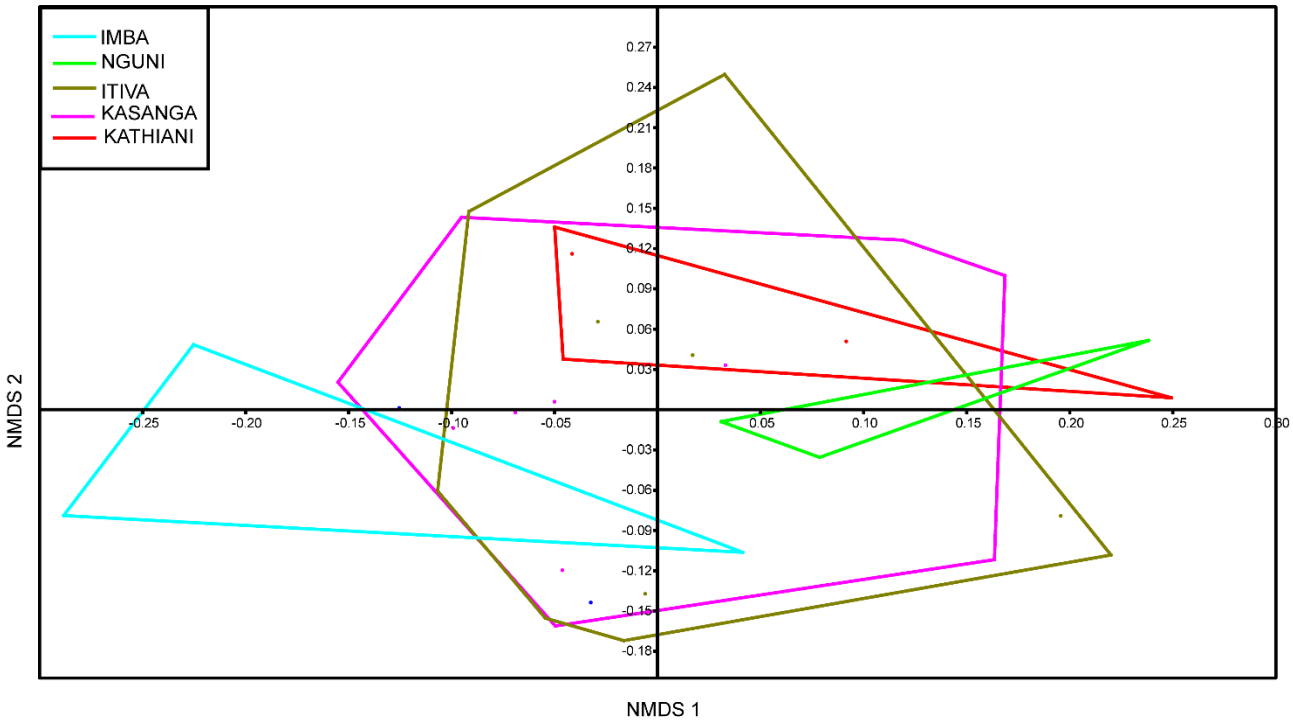

Figure 4.9: The diagram shows Non-Metric Dimensional Scaling ordination based on Bray–Curtis dissimilarities (k = 4) in pollen samples in the six study sites. The samples are distinguished and coloured by site as indicated on the figure legend.

Furthermore, Appendix E, Figure E2 shows SIMPER test results that had significant dissimilarities from the PERMANOVA test, i.e. Itiva versus Nguni (p-value =0.04) and three other pairs of sites which showed separation on the NMDS plot i.e. Imba versus Kathiani, (p-value=0.09); Imba versus Kasanga (p-value=0.09); and Imba versus Nguni (p-value=0.09); showed the plant species contributing to the separation between the sites. The plant species *Salvadora* spp., *Rhus* spp., *Leucas* spp. and *Syzygium* spp. had the most frequent contribution in separating these 4 pairs of sites.

4.3.3 Pollen protein analysis

Crude protein concentration of pollen showed no significant differences across the six sites (Kruskal-Wallis chi-squared = 3.9114, df = 5, p-value = 0.5622) as seen in Appendix E, Figure E3. In contrast, crude protein concentration across the different data collection months (May 2017, January 2018, June 2018 and November 2018) showed significant differences (Kruskal-Wallis chi-squared = 10.532, df = 3, p-value = 0.01454), (Figure 4.10). The rainfall months of May and November showed high amounts of protein concentration while the dry months of January and June showed lower amounts of protein concentration.

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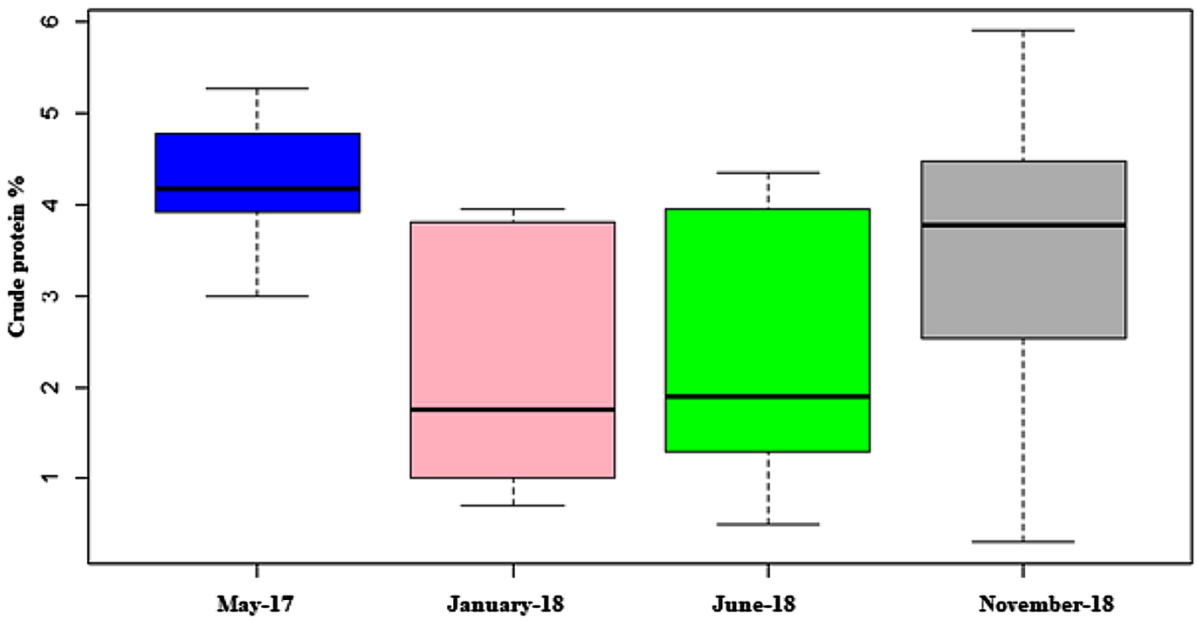

Figure 4.10: Total crude protein concentration (%) across the different months. May and November are typically the rainy seasons while January and June are dry months. Kruskal-Wallis chi-squared = 9.8298, df = 3, p-value = 0.02007. Pairwise comparisons are shown in Appendix E, Table E4.

4.4 Discussion

The outcome of the pollen analysis indicates that pollen collected from moderately degraded landscapes displayed the highest pollen diversity compared to the least degraded landscapes. This result is similar to several findings which indicated that landscape heterogeneity and diversity are positively associated with higher floral resource availability and richness (Burnett et al., 1998; Honnay et al., 2003; Statzner & Moss, 2003). Likewise, landscape heterogeneity at multiple spatial scales has been positively correlated with plant species richness (Costanza et al., 2011). This association between floral variety and landscape diversity can be explained by the habitat diversity hypothesis proposed by Shmida and Wilson (1985), whereby heterogeneous landscapes encompass additional accessible habitats and consequently, contain more species (Meltsov et al., 2013). Furthermore, it has been shown that greater landscape variety results in higher species richness (Reitalu et al., 2012). This was noted to be the case in the present study as the RAD curves indicated that low species evenness corresponded to low species diversity as demonstrated by the Renyi diversity index. Similarly, the variety of pollen in these areas suggests floral diversity which can result in disparities in pollen quality (Di Pasquale et al., 2013; Hulsmann et al., 2015) which are fundamental requirements for strong honeybee colonies. Thus, the diversity of plant species in the moderately degraded areas may provide more balanced nutrition than those from areas with fewer plant species

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as shown by Blüthgen and Klein (2011), therefore resulting in stronger colonies. Additionally, landscapes consisting of greater proportions of non-forested areas have exhibited higher floral richness than those consisting of totally closed natural/ semi-natural landscapes as well as those whose composition consisted of very little semi-natural landscapes (Billeter et al., 2008). Landscape configurational heterogeneity originating from small-scale agriculture has also been shown to contribute strongly to maintenance of pollinator communities in Europe due to the possible availing of flowering weeds from croplands (Hass et al., 2018). These weeds could be advantageous for the bees since different crops would produce different flowering weeds at various times of the year depending on crop growing seasons within the locality (Bretagnolle & Gaba, 2015), in addition to the flowering from the semi-natural habitats (Wratten et al., 2012). Hence, contributing to all year long forage availability. Moreover, plant species richness has also been shown to increase with landscape heterogeneity at the farm scale due to the presence of a variety of habitats such as arable land, open pastures and semi-natural vegetation (Weibull et al., 2003). The present study's results indicate that stronger honeybee colonies would be better supported in heterogeneous landscapes since a variety of pollen are able to provide continuous supply of forage throughout the year unlike in areas with higher plant homogeneity. In addition, I postulate that for honeybees, floral resources are more important than nesting structures since the hive is already provided by the beekeeper. Potentially therefore they would thrive more in pollen-rich heterogeneous areas which are similar to areas that are moderately degraded. This is in contrast to wild bees which require nesting structures from semi-natural areas which would be more abundant in the low degraded landscapes (Winfree et al., 2007). However, in this study, individual rarefaction curves indicated that some sites were better sampled than others (Figure 4.5). Colony absconding occurred frequently in some of the six sites (Mumoni, Kathiani and Nguni) and this could explain why the individual rarefaction curves show lower sampling effort in some sites as compared to others, and which could also contribute to the low pollen diversity seen in these areas. Moreover, there is a possibility that the diversity of plants providing resources for the bees in the study area is very high and hence an asymptote is not reached even after sampling extensively (Willott, 2001).

Additionally, this study established that only four plant species contributed to at least 50% of the cumulative number of the identified 124 plant species. This is despite observations that abundant flowering plants like the *Bougainvillea glabra* were located near the hives yet did not feature prominently amongst abundant pollen. Further, the study determined that the most abundant plants at the family level were the Capparaceae, Combretaceae and Asteraceae plant families. This is partially in agreement with the findings of Onyango et al. (2019) who in a study in a mountainous region of

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Kenya, found that the Asteraceae was amongst the most preferred melliferous plant families by the honeybee. The Fabaceae family also occurred quite frequently in this study similar to findings by Albaba (2015) who carried out a study to document important pollenifarous and nectarifarous plant species in Palestine. In a similar study in Northeastern Nigeria, Dukku (2013) found that the Fabaceae and Combretaceae families recorded the highest abundances among the plant families visited by the honeybee. Lau et al. (2019) and Brodschneider et al. (2019) also found a predominance Fabaceae and Asteraceae families in studies carried out in the United States of America and Austria, respectively. These findings points towards honeybees having pollen preferences also shown by Visscher and Seeley (1982) who found that pollen foragers showed distinct pollen preferences and targeted only a few of the available resources in their foraging vicinity. Olsen et al. (1979) also demonstrated that honeybees disregarded pollen from cucumbers and cotton fields despite their proximity to these plants. Moreover, the large overlaps which were observed in pollen composition across the six sites as represented by the NMDS results, further reinforces that there were possibly pollen preferences by the bees, leading to similarities in collected pollen across the sites. Furthermore, pollen yielded by different plant species have displayed considerable variation regarding their protein and mineral content and these variations may contribute to the pollen preferences of honeybees (Keller et al., 2005). Such qualitative differences might have a strong impact on the foraging decisions of honeybees and could possibly explain preferences for certain pollen types. Nonetheless, further experimental studies are required for this conclusion to be made (Keller et al., 2005b).

On the other hand, analysis of the crude protein percentages in pollen at both the spatial and temporal levels indicated that protein content did not vary significantly by geographical location but varied by time of collection (month). Higher protein percentages were observed in pollen during the long rainy seasons of May and November, as opposed to the dry seasons in January and June. This finding is analogous to that of de Sá-Otero et al. (2009) who found that some pollen taxa harvested by honeybees had varying amounts of protein at different dates. Steffan-Dewenter et al. (2017) also found that amount and diversity of pollen were influenced mainly by season and not by geographical location. However, these studies did not specifically analyse protein content in the pollen. This variation in protein content of honeybee bread by season may be due to the different plant species available during various seasons which affects the nutritional composition of the pollen and may also be linked to pollen preferences (Keller et al., 2005b), although more studies are required to establish this.

This study raises some fundamental questions about humans managing ecosystems sustainably. It is postulated that high plant diversity benefits beekeeping activities (i.e. maintenance of honeybee colonies for purposes of collecting hive products and for pollination), which are optimal in moderately

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disturbed areas (Mensah et al., 2017). In other parts of the world, the keeping of managed pollinators are seen as a threat to pollinator biodiversity (Garibaldi et al., 2013). Here the study shows that beekeepers should avoid completely undisturbed areas as well as highly disturbed environments, due to poorer available pollen resources. It has been shown that conservation of pollinator biodiversity and pollination services are commonly not compatible (Kleijn et al., 2015), with common bee species mostly performing most of the pollination service. Given that beekeeping is less productive in areas with minor disturbance, these areas should be seen as protecting wild pollinators. On the other hand, habitats with heterogenous plant diversity are ideal for beekeeping activities and will likely also benefit other common bee species which can provide ecosystem service. In contrast, highly degraded environments that are of limited conservation and beekeeping value should employ initiatives to improve plant diversity and vegetation cover.

4.5 Conclusions

Heterogeneous landscapes consisting of both semi-natural vegetation and croplands are shown to be most suitable for honeybees by displaying the highest pollen diversity. Pollen diversity is an important factor in ensuring strong honeybee colonies since it is the protein source for the honeybee brood and a varied pollen diet has been shown to result in healthier and stronger honeybee colonies globally. Honeybee colonies in the region should consequently be established in these heterogeneous areas for maximal benefits. However, species accumulation curves for each site did not reach an asymptote, which could indicate that the diversity of plants providing resources for the bees in the study area is very high and hence an asymptote is not reached even after sampling extensively. My results further show that three plant species i.e. *Terminalia* spp., *Cleome* spp. and *Acacia* spp dominate the pollen types collected across the six study sites, implying that honeybees could have certain preferences for these plants. Therefore, these plant species should be prioritized for conservation to ensure sustainable availability of preferred honeybee foraging resources in the region. However, protein content did not vary by location but by seasonality. Further studies consisting of more sites should be undertaken to investigate these outcomes.

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5 CHAPTER FIVE: DOES THE PRESENCE OF *VARROA DESTRUCTOR* INFLUENCE HONEYBEE COLONY STRENGTH IN FRAGMENTED LANDSCAPES?

Abstract

In recent years, honeybee (*Apis mellifera)* colony losses have escalated in most parts of the world. Factors such as habitat loss and fragmentation, pesticides, pathogens, insect pests and nutritional deficiencies have all been attributed to these colony losses. This study is the first in the region that comprehensively examines whether the degree of landscape fragmentation affects the presence of *Varroa destructor* (Varroa mite), which is a key ectoparasitic mite of the honeybee, as well as to establish whether Varroa mite abundance influences honeybee colony strength. The research was done in Kenya within six sites of varying degrees of landscape fragmentation, during the period from 2017 to 2018. Landscape fragmentation metrics were derived using fused medium resolution bi-temporal Sentinel-1 and Sentinel-2 satellite imagery. Fragmentation metrics were then extracted from six concentric buffers at intervals of 500 meters from 0.5 km to 3 km around apiaries with a study area in eastern Kenya measuring 3,773 km^2. Subsequently, two radii (1 km and 2.5 km) around each apiary were selected for the analysis. Honeybee colony strength parameters and Varroa mite data were systematically collected in a total of 69 hive inspections across all the apiaries. The results demonstrated that the proportion of croplands and patch shape index of woody vegetation positively influenced Varroa mite occurrence, while landscape fractal dimension negatively influenced Varroa mite occurrence at the 1 km radius. At the 2.5 km scale, the proportion of hedges in the landscape positively affected Varroa mite occurrence while patch sizes of hedges and the Shannon diversity index landscape metrics had a negative effect on Varroa mite occurrence. On the other hand, Varroa mite had no influence on honeybee colony strength except for number of cell eggs which were negatively affected by Varroa mite. The results suggest that Varroa mite presence has no effect on honeybee colony strength in this region and therefore synthetic Varroa mite control measures may not be recommendable or feasible. Furthermore, hive placement should carefully consider landscape structural effect as landscape fragmentation can be considered an important propagation factor for Varroa mite.

Keywords: *Varroa destructor*, landscape fragmentation, honeybees, Kenya, zero inflated negative binomial

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5.1 Introduction

Globally, intensified human activities have given rise to excessive habitat loss as a consequence of landscape fragmentation (Defries et al., 2004; Foley et al., 2005; Morris, 2010). These landscape fragments have subsequently produced isolated habitat pockets resulting in modifications of the ecological connectivity amongst landscape segments (Jaeger, 2000). One of the major effects of human-induced landscape changes are disturbances of biotic interactions, for instance those between pests and their natural enemies (Zhao et al., 2016). The consequences of these landscape interaction changes and disturbances, more often due to the expansion of agricultural lands at the expense of natural vegetation, are increased pest pressures on bee colonies (Meehan et al., 2011). Meehan et al. (2011), for instance, found that proportion and patch size of croplands resulted in increases in pest's occurrence and increased with proportion of semi-natural habitat in the landscape. Further, the proportion of woody vegetation and grassland has been shown to influence pest abundance at shorter landscape scales of 1 km to 2 km from the apiary, thereby displaying the importance of spatial scale (Rusch et al., 2013). Additionally, agricultural landscapes with larger areas of woodlots were found to have lower abundances of onion thrips pest than those with lesser amounts of woodlots (Belder et al., 2002), while landscape complexity was found to have an influence on cereal aphid densities (Roschewitz et al., 2005).

Similarly, due to landscape changes, honeybees wellbeing is challenged by a myriad threats, important among them being pests and parasites (Paudel et al., 2015; Potts et al., 2010b). The parasitic mite *Varroa destructor* (henceforth referred to as Varroa mite) is a well-known honeybee pest which forms part of multiple stressors that may affect honeybee strength (Locke et al., 2012; Rosenkranz et al., 2010; Evans & Cook, 2018). Globally, the mite is the most important threat to the apiculture industry (Yves et al., 2010; Francis et al., 2013). It has been shown to have devastating effects on honeybees (Guzman-Novoa et al., 2010; Murilhas, 2002; Delaplane & Hood, 2015) including appreciable colony mortality especially during winter seasons (Nguyen et al., 2011; Berthoud et al., 2010; van Dooremalen et al., 2012). Varroa mite has also widely been blamed for the colony collapse disorder (CCD) phenomenon in Europe and the USA (Martin, 1998; Vanengelsdorp et al., 2012). Nonetheless, the mite has not shown the same destructive effects on African honeybees which have been shown to effectively manage the mites (Muli et al., 2014; Frazier et al., 2010; Nganso et al., 2017). Additionally, environmental characteristics have been shown to have strong effects on Varroa mite infestation levels in honeybee colonies (Giacobino et al., 2017), with elevation and slope being the most common environmental factors affecting its occurrence (Correia-Oliveira et al., 2018;

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Chemurot et al., 2016; Muli et al., 2014). Further, the mites have displayed a preference for temperatures of approximately 34–35◦C (Nazzi & Conte, 2016). Likewise, intensively cultivated landscapes have exhibited significant correlation with Varroa mite presence (Dolezal et al., 2016) and spatial models have demonstrated the relationship between landcover and presence of honeybee pests including Varroa mite (Makori et al., 2017).

As far as I am aware, there is no information in Africa on the linkage between landscape fragmentation and Varroa mite levels of occurrence. There is also very little information on the connection between Varroa mite and honeybee colony strength parameters. This chapter, therefore, intends to fill this knowledge gap, while considering the proliferation of Varroa mite in Africa and rapidly changing landscapes due to global change (Mortimore et al., 2005). As such, the effects of landscape fragmentation metrics on Varroa mite occurrence were investigated in six apiaries established within distinctly varying landscapes in a study area in Kenya, as defined in Ochungo et al. (2019). Additionally, the effect of Varroa mite on honeybee colony strength parameters in the six sampling sites was examined. I sought to answer the following questions: 1) Does landscape fragmentation influence Varroa mite occurrence? and 2) Does Varroa mite abundance influence honeybee colony strength?

5.2 Methods

5.2.1 Study area

Mwingi sub-county, located in Kitui County in the eastern part of Kenya is part of the arid and semi-arid lands of Kenya and a prominent beekeeping region (Mburu et al., 2015). It is characterized by diverse landscape composition and configuration which enabled the placement of apiaries in three landscapes of varying degradation levels, as defined in Ochungo et al. (2019). Moreover, Varroa mite presence has also been recorded in studies carried out in the region (Muli et al., 2014).

The selection of the six study sites was carried out across various landscape degradation (LD) severity levels, based on abundance of natural vegetation compared with croplands as shown in Table 1 and each site was at least > 3 km from any other (Figure 5.1 and Table 5.1). Thereafter, six apiaries each comprising ten Langstroth hives (10 frames) were placed in the six locations giving a total of 60 hives. The locations of the apiaries in the landscapes are shown in Figure 5.1.

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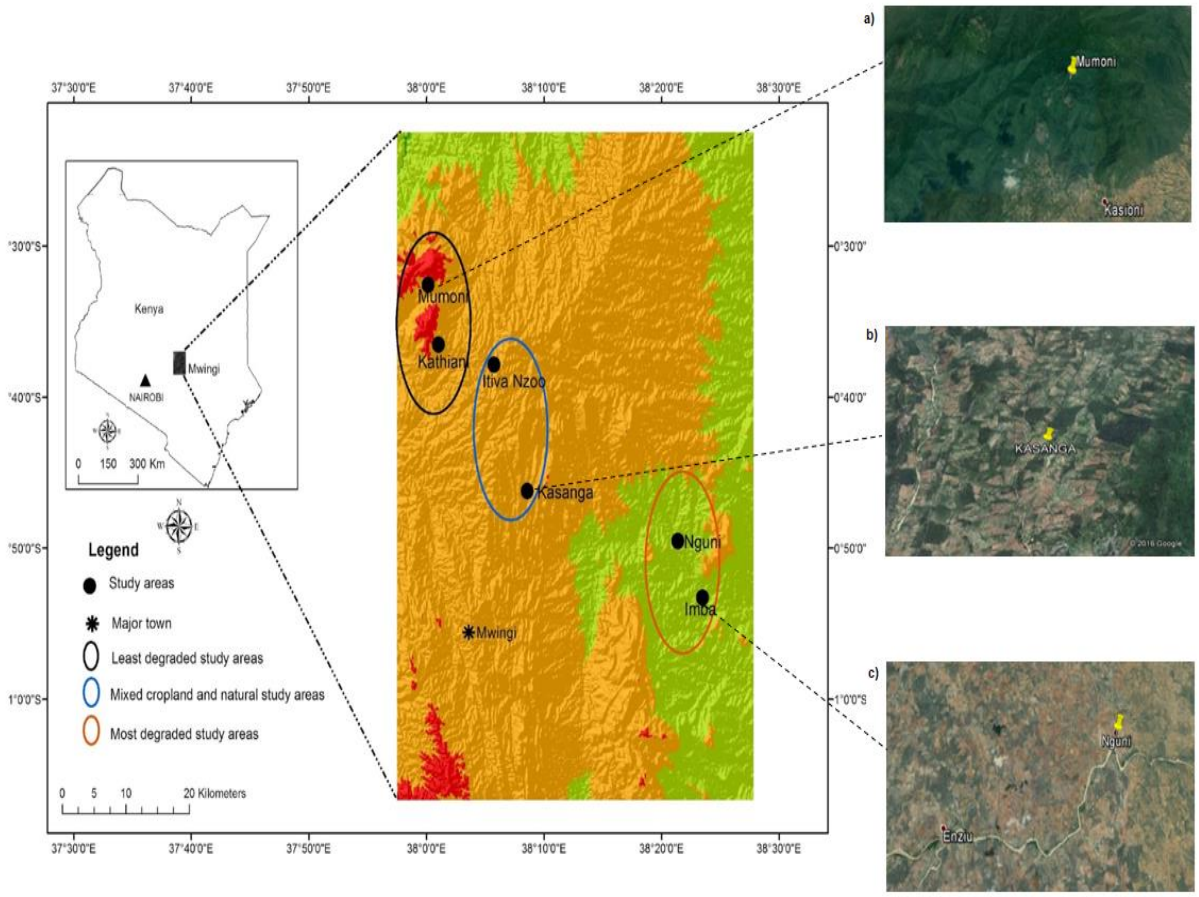

Figure 5.1: Study area in Kenya and the three 'land degradation severity' areas, indicated as ellipsoids (left). Two study sites were chosen within each of the three 'land degradation severity' areas. The orange-green shades show elevation, whereby the red shades have the highest elevation (http://dds.cr.usgs.gov/srtm/; Ochungo et al. 2019). The images on the right-hand side indicate land cover for three sites from each of the landscape degradation levels, i.e. a) least degraded, b) moderately degraded, and c) highly degraded, from top to bottom, respectively (Google maps, 2017).

5.2.2 Data collection

Landscape fragmentation metrics

Landscape fragmentation metrics were derived from fused Sentinel-1 and Sentinel-2 datasets (ESA, 2017) from six concentric buffer zones at intervals of 500 meters from 0.5 km to 3 km, around the centre of the apiaries, respectively (Ochungo et al., 2019). These metrics were chosen for use in this study based on their relevance to insect ecology traits (Hunter, 2002), and represented landscape composition, configuration, patch shape, heterogeneity, and connectedness. A total of 96 metrics at both the landscape and class levels were thereafter computed around the apiaries using the FRAGSTATS tool (Mcgarigal, 2014). In addition, the Fractional Cover of natural to croplands (FNC) index was derived and included as a measure of landscape fragmentation. The FNC index calculates

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the proportion of semi-natural vegetation to croplands in each of the study sites at the same buffers around the apiary. Essentially, a higher FNC index indicates a larger quantity of quasi natural vegetation in a site compared to another site with a lower FNC index. Consequently, a multi-collinearity assessment was carried out on the metrics using both 'findCorrelation' and Recursive Feature Elimination (RFE) bootstrapping techniques (Yan & Zhang, 2015b) in R version 3.5.3 (R core team, 2019). The 'findCorrelation' procedure consists of first conducting a Spearman's rank-order correlation test at each buffer distance scale amongst all the fragmentation parameters and, secondly, specifying a threshold of $|r| > 0.75$ to eliminate the multicollinearity (Dormann et al., 2013). Further, the RFE technique is a feature-ranking algorithm which performs optimization algorithms to achieve an optimal subset of variables by evaluating root mean square error (RMSE) values (Pullanagari et al., 2018). Subsequently, two radii were selected for the analysis i.e. 1 km to represent local foraging distances from the apiary and 2.5 km to represent the greater landscape in which the apiaries were positioned. The multi-collinearity assessment resulted in a reduced dataset at the two spatial scales as shown in Table 5.1.

Table 5.1: Fragmentation indices used to quantify the level of landscape degradation of study sites (Mcgarigal, 2014; Ochungo et al., 2019). The last column shows the metrics that were selected following the multicollinearity analysis exercise at the 1 km and 2.5 km radii. The acronyms for the fragmentation metrics are shown in brackets in the last column.

Index type	Fragstat index	Description	Selected metric
Landscape composition	Percentage of landscape (PLAND)	The proportional abundance for each of (PLAND) the patch types across the landscape	1. PLAND cropland (PLC, 1 km) 2. PLAND grassland (PLG, 2.5 km) 3. PLAND woody (PLW, 2.5 km) 4. PLAND hedges (PLH, 2.5 km)
Landscape composition	Shannon diversity index (SHDI)	Measures the number of landscape elements as well as their proportional changes. Also, the abundance of landscape types.	5. SHDI, 2.5 km

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Landscape shape	Landscape shape index (LSI)	An index used to reflect the complexity of the landscape patches; a greater value indicates more complexity	6. LSI woody (LSW, 1 km)
Landscape shape	Fractal dimension (FD)	Measures the degree of shape complexity	7. FD (1 km)
Landscape configuration	Largest patch index (LPI)	An index used to quantify the percentage of total landscape area characterized by the largest patch	8. LPI cropland (LPC, 1 km) 9. LPI hedges (LPH, 2.5 km)
Landscape composition	Fractional cover of natural to croplands (FNC)	An index which measures the proportion of semi-natural vegetation to croplands	10. FNC (1 km) 11. FNC (2 km)

Honeybee colony strength measures and Varroa mite *counts*

A total of 60 hives were placed in the six apiaries, i.e. 10 hives per apiary. However, throughout the study period, 30 hives (i.e. colonies) were inspected and sampled which were the only ones that occupied by natural swarms as observed during the first field data collection survey. Data were collected between May 2017 and November 2018, whereby the data collection was repeated 5 times between May 2017 and November 2018, during the two rainy seasons (May 2017 and November 2018) and 3 dry seasons (January 2018, February 2018 and June 2018). To estimate honeybee colony strength, methods derived from Delaplane et al. (2013b) and Imdorf and Gerig (2001) were followed after correcting for the African honeybee's body size (Buco et al., 1987) and honeycomb cell size. Both primary measures of colony strength (adult population, brood, and eggs) and secondary measures (stored pollen and honey) were methodically collected in each individual colony during the entire study period. To quantify Varroa mite load for every occupied hive at each data collection period, the sugar-dusting method following Fakhimzadeh (2001) procedure was used. Varroa mite load estimation was done from a sample of approximately 100 honeybees for each colony (n = 30) (Fakhimzadeh, 2001), calibrated using a cup of ca.430cm3 which was covered with a net on top. Confectionery sugar (5g) was then poured directly onto the sample of bees through the netted lid.

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After rolling the bees in the jar for nearly 30 seconds, the jar was then turned upside down and shaken onto a clean white paper. The bees remained inside the jar while the confectionery sugar and Varroa mite were shaken onto the paper, and the mites counted. Each hive inspection was considered as a unique data record, and only 69 hive inspections, comprising occupied hives were included in the analysis.

5.2.3 Statistical analysis

Varroa mite load count data were re-classified as presence/absence data and binary logistic generalized linear mixed effects models (GLMMs) were used to determine whether landscape fragmentation influenced Varroa mite' presence at the 1 km and 2.5 km spatial scales. Mixed effects were implemented because of the hierarchical and repetitive in situ data collections within each of the sites and colonies. The colony and site variables were therefore included in the regressions as random effects, whereby the colony variable was nested within the site variable (Chaves, 2010; Crawley, 2002). Varroa mite presence was regressed against the selected landscape fragmentation variables at both 1 km and 2.5 km spatial scales and a stepwise backward elimination of predictor variables was implemented by examining p-values and Akaike Information Criteria (AIC) values of each regression model result. Residual graphs were subsequently plotted and examined for considerable deviations.

Further, to determine whether Varroa mite abundance influenced honeybee colony strength, a zero inflated negative binomial (ZINB) regression with mixed effects was implemented. ZINB models are two-part models established for the purpose of dealing with count data which have a large quantity of zero values and exhibit over dispersion, a situation whereby count data often exhibit larger variance than the mean (Loeys et al., 2011; Sileshi, 2006). Additionally, the complete distribution of the regression result is represented by two distinct portions, a first section presenting the probability of extra zeros (logit model) and a second catering for the non- excess zeros and non-zero counts (negative binomial model) (Loeys et al, 2011; NCSS Statistical Software, 2014). On the other hand, Varroa mite abundance data were regressed against each of the honeybee colony strength parameters in separate ZINB models. The packages 'lme4' (Bates et al., 2019) and 'glmmTMB' (Magnusson et al., 2020) were used in the R-statistical programming language (R Core Team, 2019) to employ the ZINB and GLMM models, respectively. While, the package 'DHARMa' (Hartig, 2020) in the R software was used to create readily interpretable scaled residuals for the ZINB-GLMM models using QQ-plots (Quantile-Quantile plots) and included tests for accurate distribution i.e. Kolmogorov Smirnov (KS) test, dispersion and outliers.

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5.3 Results

5.3.1 Varroa mite and landscape fragmentation

The distributions of the number of Varroa mite, as a response variable, exhibited sizeable percentages of zero counts which justified the use of both the binary logistic regression and the ZINB distribution in this study. Appendix F, Figure F1 displays the distributions of Varroa mite counts.

Furthermore, scaled residuals of the binary logistic GLMMs for the Varroa mite presence/ absence response variable against the landscape fragmentation metrics at the 1 km and 2.5 km scales are shown in Appendix F, Figure F2. The QQ-plots show that overall deviations from the expected distribution were not significant thus indicating good model fits. These included tests for accurate distribution (KS test), dispersion and outliers.

Results of the mixed effects binary logistic regression to determine the effects of landscape fragmentation on Varroa mite' presence at both the 1 km and 2.5 km buffer scales are shown in Table 5.2, significant levels given by $p < 0.05$. At the 1 km buffer scale, the FD variable representing complexity of patch geometries negatively affected Varroa mite presence (p=0.00, SE = ±14.09), while the PLC variable representing the proportion of croplands in the landscape positively affected Varroa mite presence (p=0.01, SE = ± 0.23). Similarly, the LSW variable representing the largest patch shape index of woody vegetation also affected Varroa mite presence positively (p=0.03, SE = ± 0.03). On the other hand, at the 2.5 km scale, the Shannon diversity index variable, SHDI, had a negative effect on the presence of Varroa mite (p=0.00, SE = ± 1.77). Likewise, the largest patch index of hedges, LPH variable also negatively affected Varroa mite' presence (p=0.04, SE = ± 0.11). Conversely, PLH variable, had a positive effect on the presence of the mites (p=0.00, SE = ± 0.32).

Table 5.2: Binary logistic GLMM regression parameters of the response of Varroa mite presence (n = 69) to landscape fragmentation predictors at 1 km and 2.5 km radii.

Scale	Variable	Estimate	Standard error (SE ±)	z-value	
1 km	(Intercept)	68.77	22.28	3.09	*
	FD[1]	-46.11	14.09	-3.27	*
	PLC[2]	0.57	0.23	2.18	*
	LSW[3]	0.06	0.03	2.51	*
2.5km	(Intercept)	1.85	1.58	1.17	NS
	SHDI[4]	-5.20	1.77	-2.94	*

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LPH[5]	-0.23	0.11	-2.04	*
PLH[6]	1.20	0.32	3.78	*

Significance codes: <0.05 '*', > 0.05 '-'

[1]Fractal dimension; [2]Proportion of cropland; [3]Largest shape index of woody vegetation; [4]Shannon diversity index; [5]Largest patch index of hedges; [6]Proportion of hedges

5.3.2 Varroa mite and honeybee colony strength parameters

Scaled residuals for the ZINB models of Varroa mite against all colony strength parameters response variables are shown in Appendix F, Figure F3. The plots imply that overall deviations from the expected distribution, as well as tests for accurate distribution (KS test), dispersion and outliers were not significant, hence indicating good model fits.

Table 5.3 shows the results of the ZINB models of the Varroa mite abundance against each of the honeybee colony strength parameters. None of the honeybee colony strength parameters were affected by the Varroa mite abundance, except the number of egg cells, for which the Varroa mite abundance had a negative effect in the count component of the ZINB model.

Table 5.3: ZINB model parameters of the response of population of adult honeybees, cells of brood, cells of honey, cells of pollens, and cells of eggs (n = 69) to Varroa mite abundance.

		Zero component				**Count component**			
Response variable	Predictor variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
Adult honeybee population	(Intercept)	-0.23	0.19	-1.17	NS	7.86	0.11	60.41	*
	Varroa	0.09	0.06	0.12	NS	0.01	0.03	0.35	NS
Cells of brood	(Intercept)	0.47	0.20	2.38	*	8.92	0.11	80.71	*
	Varroa	0.02	0.06	0.29	NS	0.01	0.03	0.41	NS
Cells of honey	(Intercept)	0.06	0.19	0.28	NS	8.41	0.14	59.34	*
	Varroa	0.12	0.07	1.69	NS	0.07	0.07	1.04	NS
Cells of pollen	(Intercept)	0.75	0.21	3.63	*	7.84	0.15	52.17	*

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	Varroa	0.03	0.06	0.52	NS	-0.01	0.05	-0.29	NS
Cells of eggs	(Intercept)	0.84	0.21	4.00	*	7.21	0.10	72.45	*
	Varroa	0.00	0.06	-0.04	NS	-0.06	0.03	-2.24	*

Significance codes: <0.05 '*', > 0.05 'NS', NS = not significant

5.4 Discussion

The analysis showed that Varroa mite presence was influenced by landscape fragmentation variables at both the 1 km and 2.5 km spatial scales. At the 1 km scale, the negative effect of the fractal dimension variable to Varroa mite presence indicated that these mites increase with decreasing patch complexities, suggesting that simpler patch shapes influenced the presence of the mites. In this study, simpler patch shapes were found in the least degraded areas. These areas were characterized by a higher proportion of semi-natural environments with homogeneous larger patch shapes, therefore suggesting that intact semi-natural environments closer to the apiaries are favourable for Varroa mite. Also, during the study, large hive beetles (*Oplostomus fuligineus*) were observed in the least degraded areas only, which further demonstrates that these areas are more suitable for honeybee pests. This finding is similar to that of Makori et al. (2017) who reported that Varroa mite and other honeybee pests were found in areas with higher proportion of semi-natural zones. This finding may be best explained by the myriad benefits that semi-natural habitats may avail for pests by providing them shelter and a conducive habitat (Rusch et al., 2013). Besides, areas with higher proportions of semi-natural vegetation in which the mites were more prevalent were also the ones with higher elevation (~ 1000 metres above sea level) which is in agreement with findings which indicate that the mite is found in areas with higher elevation (Chemurot et al., 2016; Correia-Oliveira et al., 2018; Muli et al., 2014). Likewise, the largest shape index for the woody vegetation class positively influenced the occurrence of Varroa mite in the landscape. Rusch et al. (2013) and Zaller et al. (2008) in separate studies on insect pests found that amount of semi-natural habitats in the landscape and especially with regard to the amount of woody vegetation resulted in an increase in abundance of the pests. Again, this result is possibly due to the benefits that woody habitats are able to provide, like shelter and protection from unsuitable climatic conditions (Rusch et al., 2013). Furthermore, this study found that there was a positive effect of the proportion of croplands within the 1 km radius of the apiary on Varroa mite presence indicating that the presence of croplands encourages the mites' presence. This finding is similar to that of Meehan et al. (2011) and Dolezal et al. (2016) who found that the

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proportion of croplands within the landscape encouraged pests presence. Similarly, Zhao et al. (2016) demonstrated that pest populations and damage increased with the croplands proportions in the landscape. This is possibly due to lack of natural enemies for the pests within croplands which results in a multiplication of these pests (Haan et al., 2020).

At the 2.5 km spatial scale, the study revealed that lower Shannon diversity index (SHDI) resulted in increased presence of Varroa mite. With respect to landscape composition in the study area, the low SHDI correlated with higher natural/semi-natural land cover, which is in agreement with the findings at 1 km of the positive effect of the fractal dimension and the largest shape index of woody vegetation. Moreover, this study found that the proportion of hedges in the landscape had a positive effect on the presence of Varroa mite. This finding could be possibly linked to the connectivity role that hedges play in the environment between landscape patches. For instance, one study found that a species of pests were more abundant when hedgerows connected the croplands to the forest (Haenke et al., 2014). Another explanation for the positive effect of hedges on Varroa mite occurrence could be that the hedges are also a source of vegetation for the mites which therefore favours their occurrence (Pisani-Gareau & Shennan, 2010). Contrarily, the negative effect of the largest patch index of hedges is not clearly understood. However, it could imply that narrow hedges facilitate movement of the mites better than larger patches of hedges. This is an area that would require further research.

Regarding the effect of the number of Varroa mite on honeybee colony strength, this study found no effect on the numbers of adult honeybees, as well as brood, honey, and pollen occupied cells. This result is in agreement with studies that have been carried out in Africa (Frazier et al., 2010; Muli et al., 2014; Nganso et al., 2017; Chemurot et al., 2016). These studies found that Varroa mite had no effect on the African honeybee abundance and subsequently no interventions were currently required for Varroa mite control. Moreover, the relatively low mean Varroa mite infestation levels, 1.1 mites per 100 honeybees may also be contributing to the non-effect of the Varroa mite on the honeybee colony strength as demonstrated by Guzman-Novoa et al. (2010) and Currie & Gatien (2006). The findings of this study are interesting especially given that several recent studies in the Northern hemisphere have demonstrated that Varroa mite presence resulted in honeybee colony losses and even colony collapse disorder (Locke et al., 2012; Rosenkranz et al., 2010; Evans & Cook, 2018; Guzman-Novoa et al., 2010; Murilhas, 2002; Sammataro et al., 2000; Delaplane & Hood, 2015). However, studies previously conducted on African honeybees have revealed that African honeybees exhibit higher levels of hygienic and grooming behaviour towards the mites, as well as being less attractive to the mites compared to European honeybees (Nganso et al., 2017; Guzmán-Novoa et al., 1999). Furthermore, African honeybees frequently abscond their hives which may facilitate brood rearing

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breaks therefore reducing abundances of the mites (Fries et al., 2003). Nonetheless, it was also found that Varroa mite numbers had a negative effect on the number of cells occupied by eggs in the hive. One of the possible reasons for this finding is that Varroa mite may negatively affect eggs within the hive but due to African honeybees swarming and hygienic behaviour (Frazier et al., 2010; Muli et al., 2014; Nganso et al., 2017), this effect was ultimately not detrimental to honeybees colony strength. However, this finding requires further exploration with more targeted experiments.

Additionally, the question as to the suitability of the honeybee colony strength measures together with the landscape variables used in this study also arises. This study utilized widely acceptably and robust response variables consisting of both primary measures of honeybee colony strength i.e. number of adult honeybees and brood, as well as secondary measures i.e. quantity of stored pollen, honey and eggs (Delaplane et al., 2013). Moreover, the landscape variables utilized have also demonstrated their suitability for this study in terms of representation of landscape composition and configuration which are highly important for insect ecology (Hunter, 2002). Therefore, it is envisaged that the combination of these landscape variables and honeybee colony strength measurements can be used to indicate honeybee area suitability in regions beyond the study area and thus contribute towards broader conservation incentives and policy initiatives.

5.5 Conclusions

I show that simpler patch shapes closer to the hive as well as presence of semi-natural vegetation closer to the hives have an influence on the occurrence of the mites implying that lower fragmentation encourages the mites' presence. Higher proportions of croplands near the hives is also influential on occurrence of the mites. These two results are somewhat contradictory since they show that both semi-natural vegetation and croplands are influential on the mites' occurrence. There is a possibility that other factors such as temperature could contribute to their presence in hives. Generally, average temperatures in Mwingi are approximately 30^0C therefore would be favourable for the mites. On the other hand, I show that Varroa mites' presence has no influence on honeybee colony strength, similar to what other studies in the region have shown. This implies that honeybees in these areas have developed resistance and/or tolerance mechanisms against the Varroa mite and therefore synthetic measures may not be necessary. Pest control measures should therefore target other honeybee pests that appear to be more harmful to honeybees in the region for instance small and large hive beetles.

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6 CHAPTER SIX: LANDSCAPE FRAGMENTATION, HONEYBEE COLONY STRENGTH, POLLEN DIVERSITY AND *VARROA DESTRUCTOR* PRESENCE: A SYNTHESIS

6.1 Introduction

Landscape fragmentation and habitat loss have been demonstrated to have one of the greatest negative impacts on honeybee colonies worldwide (Kremen et al., 2002). Human-induced land transformation and specifically agricultural intensification are the main causes of landscape fragmentation, which disrupts forage availability in the landscape and therefore threatens honeybees' and other pollinators' wellbeing (Ricketts et al., 2008; Kremen et al., 2002; Steffan-Dewenter & Westphal, 2008). Research on effects of landscape fragmentation on honeybee colony strength is thus essential for comprehensive assessment of landscape composition and configuration consequences on the wellbeing of honeybees. Such evidence-based research is also critical for the establishment of livelihood strategies for beekeepers as well as integrated habitat conservation planning (Requier et al., 2019).

In Kenya and most of Africa, there is a paucity of studies specifically examining the effect of landscape fragmentation on honeybee colony strength. While linkages of honey productivity to forest proximity have been carried out in Kenya (Sande et al., 2009), as well as land cover effects on crop pollination (Gemmill-Herren & Ochieng, 2008), none of these studies have involved spatially explicit honeybee habitats linked with key aspects of honeybee wellbeing. There is thus a valid need to quantify landscape fragmentation (Aizen & Feinsinger, 1994) so as to examine its effect on honeybees colony strength, forage resources, pest occurrence and other ecological needs. This is especially critical in Africa, whose population is projected to grow faster than any other region by 2050, consequently intensifying anthropogenic effects on the natural habitat (Cohen, 2003).

In view of these knowledge gaps, I set out to examine the effect of landscape fragmentation on honeybees' colony strength in the semi-arid Mwingi area in eastern Kenya through four main related studies. I first quantified potential honeybee foraging resources and their fragmentation from landscape variables using remote sensing techniques. This study investigated the potential of newly and freely available satellite systems with high spatial resolution towards mapping of potential foraging resources required by honeybees for strong colony establishment in six selected sites with established apiaries (Chapter 2). Secondly, I proceeded to assess the influence of the fragmentation metrics of the potential foraging resources on honeybee colony strength parameters and productivity. This study also evaluated honeybee colony performance across the six apiaries with a view to determining the performance of honeybee colonies in landscapes with a gradient of fragmentation

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characteristics (Chapter 3). Thirdly, I identified plant species that were used as pollen sources for the honeybees at the six apiaries with varying degrees of landscape degradation (defined by the amount of natural vegetation within a foraging distance of the apiaries), and also determined the protein content of the pollen at the same sites. The aim of this study was to identify pollen preferences by the honeybees as well as to examine diversity of the pollen across the apiaries given the variable landscape fragmentation and degradation characteristics (Chapter 4). Finally, I studied the effect of landscape fragmentation on the occurrence of *Varroa destructor*, a key ectoparasite of honeybee populations globally. Here, I also examined the effect of the Varroa mites on honeybee colony strength parameters in the six apiaries with a view to drawing conclusions on the suitability of landscapes with varying levels of degradation on Varroa mite occurrence and whether the mite affects honeybee colonies in the region (Chapter 5).

6.2 Summary of outcomes and conclusions

The findings from my first study (Chapter 2) show that freely available high-resolution remote sensing imagery can be used to quantify potential honeybee foraging resources within heterogeneous African landscapes, as well as their degree of fragmentation. Fused imagery comprising of Sentinel-1A (SAR) and Sentinel-2A (optical) produced the highest overall classification accuracies compared to the accuracies produced by either SAR or optical imagery separately. The fusion of SAR with optical imagery has generally been shown to improve classification accuracy in classifications featuring fused images, especially since optical imagery can add spectrally rich information in the visible-NIR, as well as in the RE spectrum (Balzter et al., 2015; Abdikan et al., 2016; Torbick et al., 2017). However, the classification accuracies between the optical classification and the fused imagery classification did not differ significantly, indicating the optical imagery was more effective than SAR imagery for mapping these potential honeybee foraging resources. The spectral bands which had the highest contribution towards the ability to distinguish between the classes were the short wave infra-red (SWIR) and the newly available red-edge band regions. This indicates that band combinations targeting these important band regions should be utilized for effective mapping of potential honeybee foraging resources. Nevertheless, SAR imagery had an important contribution to the mapping exercise, producing marginally higher user's and producer's accuracies for grasslands and hedges which are under-represented but important foraging resources. The inclusion of radar has been shown to add textural landscape information for time periods that are not detectable in optical imagery because of cloud cover (Hütt et al. 2016). This implies that the role of SAR should not be disregarded in this type of mapping exercise especially because of its ability to map 'through' cloud cover and

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poor weather conditions. Furthermore, African landscapes typically consist of heterogeneous and overlapped land use land cover classes, which benefits greatly from the synergistic action of both SAR and optical imagery. These conclusions show that remote sensing can be effectively used for the spatially explicit mapping of potential foraging resources for honeybees in heterogeneous semi-arid African landscapes.

My second study (Chapter 3) further provided evidence that fragmentation metrics generated from fused SAR and optical imagery can be associated with in-situ determined honeybee colony characteristics to determine whether landscape characteristics affect honeybee colony strength. I show that simpler patch shapes closer to the hives are favourable to stronger honeybee colonies as well as higher productivity, which is similar to another study which found that forest fragment shape was the most important landscape factor affecting euglossine bee's abundance and species richness (Brosi, 2009) . Moreover, honeybees have been shown to search for the most optimal and efficient paths to return to their hives after foraging, and hence complex patch geometries would hypothetically lead to inefficient use of the honeybee's energy and consequently weaker adult workers who cannot forage effectively for pollen and nectar (Reynolds et al., 2007). Furthermore, simpler patch shapes are also associated with lower landscape fragmentation which can be important for different ecological processes (Forman, 1995). This finding implies that less fragmented areas within a close proximity to hives are advantageous to honeybees probably because they also will consist of more semi-natural vegetation which avails pollen and nectar for the honeybees. Higher fragmented areas in this study are associated with human transformed landscapes, mainly agriculture. As such, areas consisting largely of croplands will be less beneficial to honeybees. In addition, lower proportions of croplands closer to the hive are also shown to be beneficial for honeybees. This is possibly due to the seasonality of crop farming which means that crops flower for a short period and then there are no flowers available for a period of time compared to areas with semi-natural vegetation which would flower more frequently because of multiple flowering species. It has been shown that croplands proximity to hives negatively affect honeybee colony strength (Otto et al., 2016; Vaudo et al., 2012). Moreover, at the larger foraging scale, higher proportions of semi-natural vegetation and hedges are shown to be favourable for honeybee colony strength again because the variety of semi-natural vegetation will provide more pollen and nectar than croplands which flower only seasonally. Woody vegetation have been shown to provide foraging resources for the honeybees at different times of the year depending on their floral cycle (Arthur et al., 2010; Potts et al., 2010; Schrader et al., 2018) which has improved the abundance and richness of bees. An interesting finding of this study, was that honeybees located in moderately degraded landscapes which consisted of nearly equal proportions of semi-natural areas and croplands had the most consistently strong colonies throughout

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the study period, similar to other studies (Aguirre-Gutiérrez et al., 2015; Steckel et al., 2014). This pattern is analogous to the 'intermediate disturbance hypothesis' whereby pollinator species and abundance have been found to be higher in moderately disturbed landscapes compared to completely undisturbed habitats (Coulin et al., 2019; Hinners et al., 2012). This leads to the conclusion that diverse, heterogeneous landscapes could better support honeybees in these landscapes, rather than entirely natural or semi-natural landscapes. These conclusions suggest that beekeeping efforts in the region should target heterogeneous landscapes with diverse floral patterns, since they appear to avail honeybee forage from disparate land covers throughout the year (Bretagnolle & Gaba, 2015; Odoux et al., 2012). Furthermore, these types of landscapes seem to be less affected by honeybee pests such as the large hive beetle which were found in large numbers in hives situated in the least degraded areas, possibly due to presence of decaying plant matter which serve as pupating sites (Akinwande & Neumann, 2018). Honeybees in least degraded landscapes also had unexpectedly high rates of absconding, and the presence of these beetles could possibly be a reason for the honeybees' propensity to abscond.

My third study (Chapter 4) additionally suggested that heterogeneous landscapes consisting of both semi-natural vegetation and croplands are most suitable for honeybees by displaying the highest collected pollen diversity. Pollen diversity is an important factor in ensuring strong honeybee colonies since it is the protein source for the honeybee brood and a varied pollen diet has been shown to result in healthier and stronger honeybee colonies globally (Burnett et al., 1998; Honnay et al., 2003; Statzner & Moss, 2003). Importantly, the most consistently strong honeybee colonies were found in the moderately degraded landscapes as shown in Chapter 3, and these areas are also shown to have the highest pollen diversity. This implies that there may be a link between the availability of diverse pollen and strong honeybee colonies. Honeybee colonies in the region should consequently be established in these heterogeneous areas for maximal benefits. Furthermore, three plant species i.e. *Terminalia* spp., *Cleome* spp. and *Acacia* spp dominated the pollen types collected across the six study sites, implying that honeybees have certain preferences for plants. The families from which these species belong have been found to be popular with honeybees elsewhere, thus implying that they are commonly preferred by honeybees (Lau et al., 2019; Brodschneider et al., 2019). Therefore, these plant species should be prioritized for conservation to ensure sustainable availability of preferred honeybee foraging resources in the region.

My final study (Chapter 5) also showed that landscape fragmentation has an influence on occurrence of *Varroa destructor*, a key ectoparasite of the honeybee. Once again, I show that simpler patch shapes closer to the hive as well as presence of semi-natural vegetation closer to the hives has an

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influence on the occurrence of the mites, similar to other studies (Rusch et al., 2013; Makori et al., 2017). Higher proportions of croplands near the hives also affected the occurrence of mites. These two results are somewhat contradictory since they show that both semi-natural vegetation and croplands are influential on the mites' occurrence. Whereas ecological evidence exists that support the presence of Varroa mites in vegetated areas (Akinwande & Neumann, 2018), the influence of croplands on the presence of Varroa mites is less clear. There is a possibility that other factors such as temperature could contribute to their likely presence in hives which are located close to croplands, particularly since temperatures of ~ 34^{o}C have been shown to be favourable for the presence of Varroa mites (Nazzi & Conte, 2016). Generally, average temperatures in Mwingi are approximately 30^{o}C therefore would be favourable for the mites. On the other hand, I show that Varroa mites presence had no influence on honeybee colony strength, like what other studies in the region have shown (Frazier et al., 2010; Muli et al., 2014; Nganso et al., 2017; Chemurot et al., 2016). This implies that honeybees in these areas have developed resistance and/or tolerance mechanisms against the Varroa mite and therefore use of synthetic control methods may not be necessary (Frazier et al., 2010). Pest control measures should therefore target other honeybee pests that appear to be more harmful to honeybees in the region, e.g. small and large hive beetles (Muli et al., 2014).

6.3 Study recommendations and limitations

Future research opportunities could be found in the validation of the mapping methods used in this study into other regions of Kenya and in Africa. This could be done for determining landscape elements which are crucial for honeybees foraging, deriving fragmentation levels of these areas and for the establishment of the suitability of these methods for the identification of suitable regions for honeybee keeping in semi-arid areas in Kenya and Africa. The following paragraphs discuss recommendations that can therefore be contemplated for future work.

The availability of new and freely available satellite images with higher acquisition frequencies globally (Sudmanns et al., 2020) presents new opportunities for quantification of landscape fragmentation in Africa and other regions. This therefore enables the expansion of the mapping methodologies used in this dissertation to a wider regional scale for fit-for-purposes monitoring of honeybee colony performance as a function of landscape fragmentation. Fusion of recent and freely available high resolution optical and SAR remote sensing imagery was found to perform better than the individual satellite images used for mapping fine-scaled landscape structural elements (which are key honeybee habitats). The fused mapping model could be expanded to the rest of Kenya and Africa, where land use/cover classes are primarily heterogeneous and overlapped, thus presenting an inherent

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difficulty in its mapping and quantification (Brosi et al., 2008). Undeniably, higher resolution remote sensing imagery like the one-metre resolution PLANET data (Planet Labs Inc., 2020), may be better for monitoring such honeybee habitats with respect to fragmentation levels. However, the increased detail may also introduce more 'artifacts' (spectral confusion) in the image interpretation (Moran, 2010). Thus, potential future studies could also unearth valuable linkages between honeybee colonies and other landscape and environmental factors such as elevation and topography. In summary, novel studies could develop the evaluation of honeybee responses to changes in the landscape by incorporating various study regions, spatial and temporal resolutions, and analysis of honeybee responses (Galbraith et al., 2015).

Landscape fragmentation metrics at various buffer zones that were used in this study could be used to inform hive placement so as to evaluate honeybee colony performance and therefore validate the methods that were applied in this study to determine honeybee colony strength in various landscape degradation gradients. Overall, honeybee colonies in this study were stronger in the moderately degraded and heterogeneous landscapes consisting of balanced proportions of natural/ semi-natural landscapes (woody vegetation, grasslands and hedges) and croplands. Moreover, pollen diversity was also higher in these moderately degraded and heterogeneous landscapes. Synthesized findings from several studies globally indicate that more heterogeneous landscapes support a variety of pollinator communities with higher floral diversity and hence are able to support diverse crops and wild plants (IPBES, 2016). Honeybee hives could be placed in such areas, and performance observed.

Monitoring of the occurrence of honeybee pests like the small and large hive beetles which affect beekeepers in Kenya could be undertaken while considering the landscape fragmentation metrics which were found to affect Varroa mite presence. This would be done to establish landscape suitability for these pests and ultimately plan for management strategies for these pests. In this study, areas with landscape homogeneity consisting of natural/ semi-natural landscapes, were shown to increase the occurrence of Varroa mites, which corroborates with other findings (Makori et al., 2017; Rusch et al., 2013; Zaller et al., 2008). This further confirms that the fragmentation mapping method used in this study is reliable and can be applied to monitor honeybee pests in other geographical settings. Furthermore, the method used for Varroa mite estimation reinforced what other research has shown, that honeybees in this region are not negatively impacted by Varroa mite (Chemurot et al., 2016; Frazier et al., 2010; Muli et al., 2014; Nganso et al., 2017). This finding ratifies the robustness of the methodology used in this study for estimation of honeybee colony strength parameters as well

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as Varroa mite estimation and similar approaches for honeybee pest monitoring can be applied in other regions in Kenya and Africa.

In Kenya, documentation on the suitability of landscapes with various fragmentation levels for honeybee keeping is lacking. For instance, beekeepers in least degraded areas with plenty of natural/ semi-natural vegetation should be made aware of the higher possibility of infestation with honeybee pests and therefore the need for mitigation measures. Furthermore, heterogeneous landscapes with diverse forage from both natural/semi-natural vegetation and croplands can be recommended for honeybee keeping as opposed to homogeneous landscapes with either excessive natural/seminatural vegetation or excessive croplands and degradation as shown in this study. Moreover, the protocol used in this study for monitoring honeybees' colony strength has proved to be robust and could be scaled to the rest of the country and possibly to the continent. Emphasis needs to be placed on the integration of remote sensing methods for landscape quantification and hive inspections for the establishment of colony status (Galbraith et al., 2015). Additionally, given the high rate of absconding of honeybees in Africa (Carroll, 2006; Pirk et al., 2016), which was experienced in this study as well, it can be recommended that supplementary feeding of honeybees with sugar syrup during seasons of nectar and pollen dearth. This could sustain the bees and possibly prevent resource-induced absconding until the season changes (Honey Bee Health Coalition, 2019). Furthermore, the presence of pests may also contribute to disturbance-induced absconding (Spiewok et al., 2006) and therefore the use of novel non-chemical pest management practices (traps) (Stief et al., 2020) could also be incorporated to reduce this type of absconding. Likewise, it will be useful if policies which discourage excessive landscape fragmentation could be implemented since it has been shown in this study that apiaries located in the highly fragmented landscapes performed poorly throughout the study period. This would assist the beekeepers to conserve the environment as well as possibly improve their livelihoods through increased hive productivity.

Limitations of this study mainly lie in the relatively low number of study areas per landscape degradation area. While the results of this study correspond to several others globally (Burnett et al., 1998; Honnay et al., 2003; Statzner & Moss, 2003), this study was limited to six experimental sites, which might limit generalizations to other regions. The integration of landscape fragmentation with honeybee colony strength observations is nonetheless a crucial research area that could be scaled out and investigated in other regions. Additionally, it would have been desirable to carry out the study for a longer duration to examine whether the same effects would be observed in the honeybee colonies. Likewise, the buffer radius was limited to 3 km per study apiary based on the foraging range established in Vaudo et al. (2012) which indicated that African honeybees typically forage within 1

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km of the hive. However, it would be interesting to expand these buffer zones to larger radii and thereafter derive fragmentation metrics which would be linked to honeybee colony strength parameters so as to determine whether fragmentation at longer distances from the hive will affect honeybee colony strength.

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APPENDIX A: HONEYBEE COLONY STRENGTH DATA

Site	Colony	Month	Popbees	Cellsbrood	Cellshoney	Cellspollen	Cellseggs
Imba	1	May	2934	440	0	880	440
Imba	2	May	2075	0	2639	440	0
Imba	1	January	2617	0	0	0	0
Imba	2	January	0	0	0	0	0
Imba	1	February	349	4400	1320	1980	2200
Imba	2	February	0	0	0	0	0
Imba	3	February	0	0	0	0	0
Imba	1	June	2816	9680	3520	2640	1540
Imba	2	June	0	0	0	0	0
Imba	3	June	0	0	0	0	0
Imba	1	November	1745	4180	1980	0	440
Imba	2	November	0	0	0	0	0
Imba	3	November	0	0	0	0	0
Imba	3	January	0	0	0	0	0
Imba	3	May	714	220	440	0	1320
Imba	4	May	845	0	0	0	0
Imba	4	January	0	0	0	0	0
Imba	4	February	0	0	0	0	0
Imba	4	June	0	0	0	0	0
Imba	4	November	0	0	0	0	0
Itiva Nzoo	1	May	581	11733	10560	4180	1100
Itiva Nzoo	2	May	1411	12247	11953	3007	1100
Itiva Nzoo	1	January	1348	0	2860	220	0
Itiva Nzoo	2	January	1220	0	1540	0	0
Itiva Nzoo	3	January	2105	0	88	0	0
Itiva Nzoo	4	January	0	0	0	0	0
Itiva Nzoo	1	February	1126	5500	5500	4180	1540
Itiva Nzoo	2	February	2792	7700	2860	0	0
Itiva Nzoo	3	February	793	5500	1760	440	2200
Itiva Nzoo	4	February	0	0	0	0	0
Itiva Nzoo	1	June	5893	0	7480	0	0
Itiva Nzoo	2	June	2617	2200	2200	1540	1100
Itiva Nzoo	3	June	5155	1540	25300	7700	220
Itiva Nzoo	4	June	0	0	0	0	0
Itiva Nzoo	1	November	4759	14740	440	1320	0
Itiva Nzoo	2	November	2538	15180	0	1320	440
Itiva Nzoo	3	November	0	0	0	0	0
Itiva Nzoo	4	November	0	0	0	0	0
Itiva Nzoo	3	May	5869	19580	4400	2200	880
Itiva Nzoo	4	May	1824	8360	0	880	440
Kasanga	1	May	3759	9211	8323	0	1100
Kasanga	2	May	1951	9636	5045	3608	1980

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Kasanga	3	May	4759	6996	2567	0	1100
Kasanga	4	May	1925	4209	1943	0	1100
Kasanga	5	May	3463	11000	4840	1760	0
Kasanga	6	May	3468	12320	5317	1100	1100
Kasanga	7	May	909	5456	2713	0	0
Kasanga	8	May	4780	9863	4693	0	1100
Kasanga	1	January	3034	0	0	0	0
Kasanga	2	January	0	0	0	0	0
Kasanga	3	January	3807	0	44	0	0
Kasanga	4	January	4227	0	0	0	0
Kasanga	5	January	1729	0	0	0	0
Kasanga	6	January	2823	0	880	0	0
Kasanga	7	January	0	0	0	0	0
Kasanga	8	January	0	0	0	0	0
Kasanga	1	February	793	7260	1760	3520	3080
Kasanga	2	February	0	0	0	0	0
Kasanga	3	February	777	7700	4620	5280	3300
Kasanga	4	February	761	6380	2860	3520	1100
Kasanga	5	February	0	0	0	0	0
Kasanga	6	February	611	10120	6160	3960	1540
Kasanga	7	February	0	0	0	0	0
Kasanga	8	February	0	0	0	0	0
Kasanga	1	June	2578	6600	0	0	0
Kasanga	2	June	0	0	0	0	0
Kasanga	3	June	10945	4620	12100	440	1980
Kasanga	4	June	8565	14300	11000	660	0
Kasanga	5	June	0	0	0	0	0
Kasanga	6	June	611	2200	0	0	0
Kasanga	7	June	0	0	0	0	0
Kasanga	8	June	0	0	0	0	0
Kasanga	1	November	1348	3960	220	220	440
Kasanga	2	November	0	0	0	0	0
Kasanga	3	November	4917	18260	6820	6380	440
Kasanga	4	November	3886	9900	8580	1760	880
Kasanga	5	November	0	0	0	0	0
Kasanga	6	November	0	0	0	0	0
Kasanga	7	November	0	0	0	0	0
Kasanga	8	November	0	0	0	0	0
Kathiani	1	May	2390	10824	12540	587	3300
Kathiani	2	May	608	1540	0	0	1100
Kathiani	3	May	6657	8287	2640	0	2200
Kathiani	4	May	1602	3080	1613	0	1100
Kathiani	5	May	2882	4987	3813	1613	1100
Kathiani	1	January	1983	0	11000	0	0
Kathiani	2	January	0	0	0	0	0
Kathiani	3	January	1348	0	1980	0	0

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Kathiani	4	January	0	0	0	0	0
Kathiani	5	January	0	0	0	0	0
Kathiani	1	February	3783	0	0	0	0
Kathiani	2	February	0	0	0	0	0
Kathiani	3	February	4124	4840	3080	4400	440
Kathiani	4	February	0	0	0	0	0
Kathiani	5	February	4838	3828	10120	2684	0
Kathiani	1	June	0	0	0	0	0
Kathiani	2	June	0	0	0	0	0
Kathiani	3	June	0	0	0	0	0
Kathiani	4	June	0	0	0	0	0
Kathiani	5	June	0	0	0	0	0
Kathiani	1	November	0	0	0	0	0
Kathiani	2	November	0	0	0	0	0
Kathiani	3	November	0	0	0	0	0
Kathiani	4	November	0	0	0	0	0
Kathiani	5	November	0	0	0	0	0
Mumoni	1	February	6979	12760	3520	4400	880
Mumoni	1	January	5435	9650	2550	3200	650
Mumoni	2	January	3252	5720	1320	660	440
Mumoni	1	June	0	0	0	0	0
Mumoni	1	May	2506	12760	13713	7773	2200
Mumoni	1	November	0	0	0	0	0
Mumoni	2	February	1015	1100	660	0	0
Mumoni	3	January	0	0	0	0	0
Mumoni	4	January	0	0	0	0	0
Mumoni	2	June	0	0	0	0	0
Mumoni	2	May	1406	6453	4767	6013	1100
Mumoni	2	November	0	0	0	0	0
Mumoni	3	February	0	0	0	0	0
Mumoni	3	May	423	0	660	0	0
Mumoni	4	February	0	0	0	0	0
Mumoni	4	May	2538	12833	21707	5060	1100
Mumoni	3	June	0	0	0	0	0
Mumoni	4	June	0	0	0	0	0
Mumoni	3	November	0	0	0	0	0
Mumoni	4	November	0	0	0	0	0
Nguni	1	May	1636	0	0	0	0
Nguni	2	May	1071	0	1027	953	0
Nguni	3	May	1243	0	2713	0	0
Nguni	4	May	2194	0	440	440	0
Nguni	5	May	1639	0	880	220	0
Nguni	1	January	2459	0	5500	440	0
Nguni	2	November	0	0	0	0	0
Nguni	3	January	0	0	0	0	0
Nguni	4	January	0	0	0	0	0

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Nguni	5	January	0	0	0	0	0
Nguni	1	November	0	0	0	0	0
Nguni	2	February	0	0	0	0	0
Nguni	3	February	0	0	0	0	0
Nguni	4	February	0	0	0	0	0
Nguni	5	February	0	0	0	0	0
Nguni	1	June	0	0	0	0	0
Nguni	2	June	0	0	0	0	0
Nguni	3	June	0	0	0	0	0
Nguni	4	June	0	0	0	0	0
Nguni	5	June	0	0	0	0	0
Nguni	2	January	1903	6820	3960	1760	440
Nguni	2	February	1269	1320	1320	0	0
Nguni	3	November	0	0	0	0	0
Nguni	4	November	0	0	0	0	0
Nguni	5	November	0	0	0	0	0

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APPENDIX B: POLLEN IDENTIFICATION DATA

Species/sample#	Family	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Acanthaceae indet.	Acanthaceae	13	0	0	0	3	0
Blepharis	Acanthaceae	1	0	0	0	0	0
Hypoestes	Acanthaceae	3	23	335	56	1	1
Penstrophe	Acanthaceae	2	0	13	0	2	0
Achyranthes	Acanthaceae	88	0	0	0	0	0
Justicia	Acanthaceae	25	4	22	70	5	8
Hygrophilia	Acanthaceae	12	44	43	0	0	3
Trianthera	Aizoaceae	0	0	0	3	0	0
Aloe	Aloeceae	0	19	1	129	1	1
Aerva	Amar/Cheno	2	0	0	0	0	0
Amaranth/Cheno	Amar/Cheno	7	16	369	174	0	32
Lannea	Anacardiaceae	5	60	0	0	46	0
Rhus	Anacardiaceae	107	0	0	117	444	0
Sclerocarya	Anacardiaceae	0	11	72	0	1	0
cf. Heromorpha	Apiaceae	0	0	0	0	0	167
Adenium	Apocynaceae	0	0	7	32	0	0
Hyphaene	Aracaceae/Palmae	0	11	0	15	42	131
Asclepidiaceae	Asclepidiaceae	0	0	1	0	0	0
Ageratum	Asteraceae	2	3	0	0	2	0
Asteraceae Indet	Asteraceae	5	0	7	0	0	0
Apilia	Asteraceae	361	24	116	41	195	8
Eclipta	Asteraceae	194	0	0	0	0	0
Elephantopus	Asteraceae	0	0	0	0	1	0
Sphaelanthus	Asteraceae	32	0	0	0	0	0
Stoebe	Asteraceae	0	0	0	1179	0	125
Tagetes	Asteraceae	34	0	0	0	0	0

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Appendix B continued

Species/sample#	Family	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Tarchonanthus	Asteraceae	0	0	2	0	71	0
Vernonia	Asteraceae	255	5	108	5	473	199
Balanites	Balanitaceae	0	0	0	21	7	0
Bombax	Bombacaceae	0	0	0	6	0	0
Cordia	Boraginaceae	1	0	3	14	2	0
Heliotropium	Boraginaceae	3	3	0	58	8	55
Brassicaceae	Brassicaceae	0	0	7	3	0	4
Boswellia	Burseraceae	0	0	0	0	4	1
Boscia	Capparaceae	0	33	13	33	126	10
Capparaceae indet	Capparaceae	2	0	0	25	0	1
Capparis	Capparaceae	0	0	0	1225	346	0
Cleome	Capparaceae	24	51	1188	831	8	11
Leonotis	Capparaceae	60	0	50	0	6	2
Maerua	Capparaceae	1	12	0	0	0	0
Parinari	Chrysobalanceae	0	0	0	0	0	15
Commiphora	Combretaceae	46	0	355	7	2	275
Terminalia	Combretaceae	0	1942	0	596	355	2
Commelina	Commelinaceae	0	7	11	0	0	0
Ipomea	Convulvulaceae	22	0	54	26	0	9
Cucumis	Cucurbutaceae	31	6	567	0	0	2
Momordica	Cucurbutaceae	0	0	0	4	6	0
Cyperus	Cyperaceae	0	110	6	0	0	0
Dracaena	Dracenaceae	0	0	0	0	0	5
Acalypha	Euphorbiaceae	2	7	21	6	64	0
Alchornea	Euphorbiaceae	0	2	0	0	5	14
Croton	Euphorbiaceae	3	15	1	13	13	1

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Appendix B continued

Species/sample#	Family	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Euphorbia	Euphorbiaceae	33	10	23	32	28	280
Phyllanthus	Euphorbiaceae	40	174	300	15	10	0
Ricinus	Euphorbiaceae	0	15	5	10	0	0
Acacia	Fabaceae	84	44	634	166	50	1046
Albizia	Fabaceae	9	0	0	5	0	0
Combretum	Fabaceae	0	56	12	52	24	0
Delonix	Fabaceae	0	0	1	33	14	2
cf. Hypericum	Hypericaceae/Guttiferae	8	0	0	0	0	0
Indet	Indet	0	0	0	2	0	0
Basilicum	Labiateae/Lamiaceae	0	0	0	8	0	0
Leucas	Labiateae/Lamiaceae	595	0	6	5	5	397
Ocimum	Labiateae/Lamiaceae	5	13	60	78	0	2
Chlorophytum	Liliaceae	0	0	0	6	0	61
Loranthus	Loranthaceae	0	0	1	0	0	26
Ammania	Lythraceae	0	39	0	43	0	0
Abutilon	Malvaceae	0	0	0	53	0	0
Hibiscus	Malvaceae	49	6	20	2	7	16
Pavonia	Malvaceae	0	0	0	0	1	16
Sida	Malvaceae	0	0	0	1	0	0
Melia	Meliaceae	0	0	0	0	6	0
Melia	Meliaceae	0	38	15	0	0	0
Mimosa	Mimosaceae	0	0	0	0	4	0
Bosquea/Trilepisium	Moraceae	5	0	0	0	0	0
Ficus	Moraceae	1	0	3	0	0	0
Maesa	Myrsinaceae	0	0	1	0	0	0
Syzygium/Eucalyptus	Myrtaceae	0	7	11	4	6	658

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Appendix B continued

Species/sample#	Family	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Boerhavia	Nyctaginaceae	0	0	4	1	4	6
Boungainvillea	Nyctaginaceae	1	0	0	0	0	0
Ximenia	Olacaceae	0	0	0	0	3	0
Olea	Oleaceae	13	18	5	28	0	0
Crotaralia	Papilionaceae	24	0	0	11	0	1
Indigofera	Papilionaceae	75	41	231	10	148	0
Legume indet	Papilionaceae	2	1	18	0	15	3
Rhynochosia	Papilionaceae	2	8	6	8	169	0
Sesbania	Papilionaceae	5	0	15	7	0	0
Tamaridus	Papilionaceae	0	0	0	0	5	0
Tephrosia	Papilionaceae	0	0	4	3	0	16
Vigna	Papilionaceae	1	0	0	0	0	0
Pittosporum	Pittosporaceae	0	0	0	0	0	1
Cereals (Millet/sorghum)	Poaceae	209	0	0	0	14	0
Poaceae	Poaceae	177	1	375	55	162	168
Zea Mays	Poaceae	6	4	0	0	0	4
Polygonum	Polygonaceae	1	0	1	6	19	0
Rumex	Polygonaceae	0	0	0	0	3	1
Protea	Proteaceae	0	1	0	0	0	0
Ziziphus	Rhamnaceae	0	61	0	0	0	0
Juniperus	Rosaceae	0	0	6	0	0	0
Anthocleista	Rubiaceae	0	0	0	0	0	61
Anthospermum	Rubiaceae	0	0	12	3	0	0
Canthium	Rubiaceae	0	3	0	1	0	1
Lepidangathus	Rubiaceae	1	0	0	0	0	0
Psychotria	Rubiaceae	0	12	4	7	0	0

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Appendix B continued

Species/sample#	Family	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Rubiaceae indet	Rubiaceae	0	0	0	8	5	0
Rutaceae	Rutaceae	33	0	0	7	0	0
Vepris	Rutaceae	0	0	0	4	0	0
Salvadora	Salvadoraceae	9	67	221	12	632	0
Allophyllus	Sapidaceae	0	0	0	0	0	4
Sapindaceae	Sapidaceae	0	0	65	0	0	4
Stemodia	Schlorophulaceae	5	0	0	1	0	89
Stemodia	Schlorophulaceae	0	1	0	0	3	0
Striga	Schlorophulaceae	0	0	0	0	1	0
Tragia	Schlorophulaceae	3	0	0	0	0	0
Solanum	Solanaceae	5	24	33	26	3	34
Steculia	Steculiaceae	0	0	0	1	0	0
Corchorus	Tiliaceae	29	1	0	0	68	7
Grewia	Tiliaceae	28	54	338	255	128	133
Typha	Typhaceae	0	0	0	0	0	1
Celtis	Ulmaceae	0	0	4	27	0	37
Unknown	Unknown	0	1	5	0	0	4
Cardiospermum	Verbanaceae	5	6	4	0	0	140
Cassia	Verbanaceae	4	0	0	0	0	1
Cissus	Verbanaceae	0	0	0	0	0	5
Tribulus	Zygophyliaceae	0	0	0	0	7	0

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APPENDIX C: CRUDE PROTEIN CONTENT OF POLLEN

Origin	Tube	Weight	Volume	Abs	ug/ml	ug/g	mg/g	% /g/100g
KAS 05 May 2017	1A	0.025	4	0.71	231.31	37010	37.01	3.70
	1B	0.025	4	0.82	266.63	42660	42.66	4.27
	1C	0.025	4	0.73	240.06	38410	38.41	3.84
Mumoni May 2017	2A	0.025	4	0.65	213.19	34110	34.11	3.41
	2B	0.025	4	0.49	164.75	26360	26.36	2.64
	2C	0.025	4	0.55	182.25	29160	29.16	2.92
Itiva May 2017	3A	0.025	4	0.69	227.25	36360	36.36	3.64
	3B	0.025	4	0.75	246.31	39410	39.41	3.94
	3C	0.025	4	0.74	243.19	38910	38.91	3.89
Nguni May 2017 I	4A	0.025	4	1.17	376.63	60260	60.26	6.03
	4B	0.025	4	0.91	296.00	47360	47.36	4.74
	4C	0.025	4	0.96	310.06	49610	49.61	4.96
Nguni May 2017 II	5A	0.025	4	0.83	270.06	43210	43.21	4.32
	5B	0.025	4	0.95	308.81	49410	49.41	4.94
	5C	0.025	4	0.70	228.50	36560	36.56	3.66
Imba May 2017	6A	0.025	4	0.90	291.94	46710	46.71	4.67
	6B	0.025	4	0.91	294.13	47060	47.06	4.71
	6C	0.025	4	0.96	309.75	49560	49.56	4.96
Kathiani May 2017	7A	0.025	4	0.85	276.94	44310	44.31	4.43
	7B	0.025	4	0.98	316.63	50660	50.66	5.07
	7C	0.025	4	0.94	304.44	48710	48.71	4.87
Kasanga 01 Nov 2018	8A	0.025	4	0.77	252.25	40360	40.36	4.04
	8B	0.025	4	0.69	226.94	36310	36.31	3.63
	8C	0.025	4	-	-	-	-	-
Itiva 02 Nov 2018	9A	0.025	4	1.46	467.25	74760	74.76	7.48
	9B	0.025	4	0.63	207.56	33210	33.21	3.32
	9C	0.025	4	0.64	210.38	33660	33.66	3.37
Kasanga 03 Nov 2018	10A	0.025	4	0.72	236.00	37760	37.76	3.78
	10B	0.025	4	0.80	260.69	41710	41.71	4.17
	10C	0.025	4	1.04	335.69	53710	53.71	5.37
Kas 02 Nov 2018	11A	0.025	4	0.60	197.25	31560	31.56	3.16
	11B	0.025	4	0.60	199.44	31910	31.91	3.19
	11C	0.025	4	0.71	232.25	37160	37.16	3.72
Itiva 02 Nov 2018	12A	0.025	4	0.63	206.31	33010	33.01	3.30
	12B	0.025	4	0.61	201.31	32210	32.21	3.22
	12C	0.025	4	0.78	254.75	40760	40.76	4.08
Itiva 03 Nov 2018	13A	0.025	4	0.63	208.19	33310	33.31	3.33
	13B	0.025	4	0.71	234.13	37460	37.46	3.75
	13C	0.025	4	0.78	255.38	40860	40.86	4.09
Kasanga 05 Jan 2018	14A	0.025	4	0.83	269.13	43060	43.06	4.31
	14B	0.025	4	0.54	180.38	28860	28.86	2.89
	14C	0.025	4	0.81	264.44	42310	42.31	4.23

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Mumoni 01 June 2018	15A	0.025	4	0.66	216.63	34660	34.66	3.47
	15B	0.025	4	0.73	239.75	38360	38.36	3.84
	15C	0.025	4	0.87	283.50	45360	45.36	4.54
Itiva 01 Nov 2018	16A	0.025	4	1.05	337.56	54010	54.01	5.40
	16B	0.025	4	1.24	396.94	63510	63.51	6.35
	16C	0.025	4	1.16	371.94	59510	59.51	5.95
Kasanga 06 May 2017	17A	0.025	4	0.74	240.69	38510	38.51	3.85
	17B	0.025	4	0.82	266.00	42560	42.56	4.26
	17C	0.025	4	0.73	239.13	38260	38.26	3.83
Itiva May 2017	18A	0.025	4	0.77	252.88	40460	40.46	4.05
	18B	0.025	4	0.85	277.88	44460	44.46	4.45
	18C	0.025	4	0.77	252.56	40410	40.41	4.04
Nguni 01 Nov 2018	19A	0.025	4	0.76	248.50	39760	39.76	3.98
	19B	0.025	4	0.88	284.75	45560	45.56	4.56
	19C	0.025	4	0.71	232.25	37160	37.16	3.72
Kasanga May 17	20A	0.025	4	0.67	219.44	35110	35.11	3.51
	20B	0.025	4	0.88	286.63	45860	45.86	4.59
	20C	0.025	4	0.69	227.25	36360	36.36	3.64
Kasanga November 2018	21A	0.025	4	0.76	246.94	39510	39.51	3.95
	21B	0.025	4	0.90	293.19	46910	46.91	4.69
	21C	0.025	4	0.95	308.19	49310	49.31	4.93
June 2018 Itiva 02	22A	0.025	4	0.76	249.13	39860	39.86	3.99
	22B	0.025	4	0.87	283.19	45310	45.31	4.53
	22C	0.025	4	0.87	282.56	45210	45.21	4.52
Kathiani 01 May 2017	23A	0.025	4	0.97	315.06	50410	50.41	5.04
	23B	0.025	4	1.06	341.94	54710	54.71	5.47
	23C	0.025	4	1.03	331.63	53060	53.06	5.31
	24A	0.025	4	1.11	356.31	53581	53.58	5.36
Kathiani Jan 2018	24B	0.025	4	0.92	299.44	30246	30.25	3.02
	24C	0.025	4	0.79	258.81	34740	34.74	3.47

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APPENDIX D: CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES

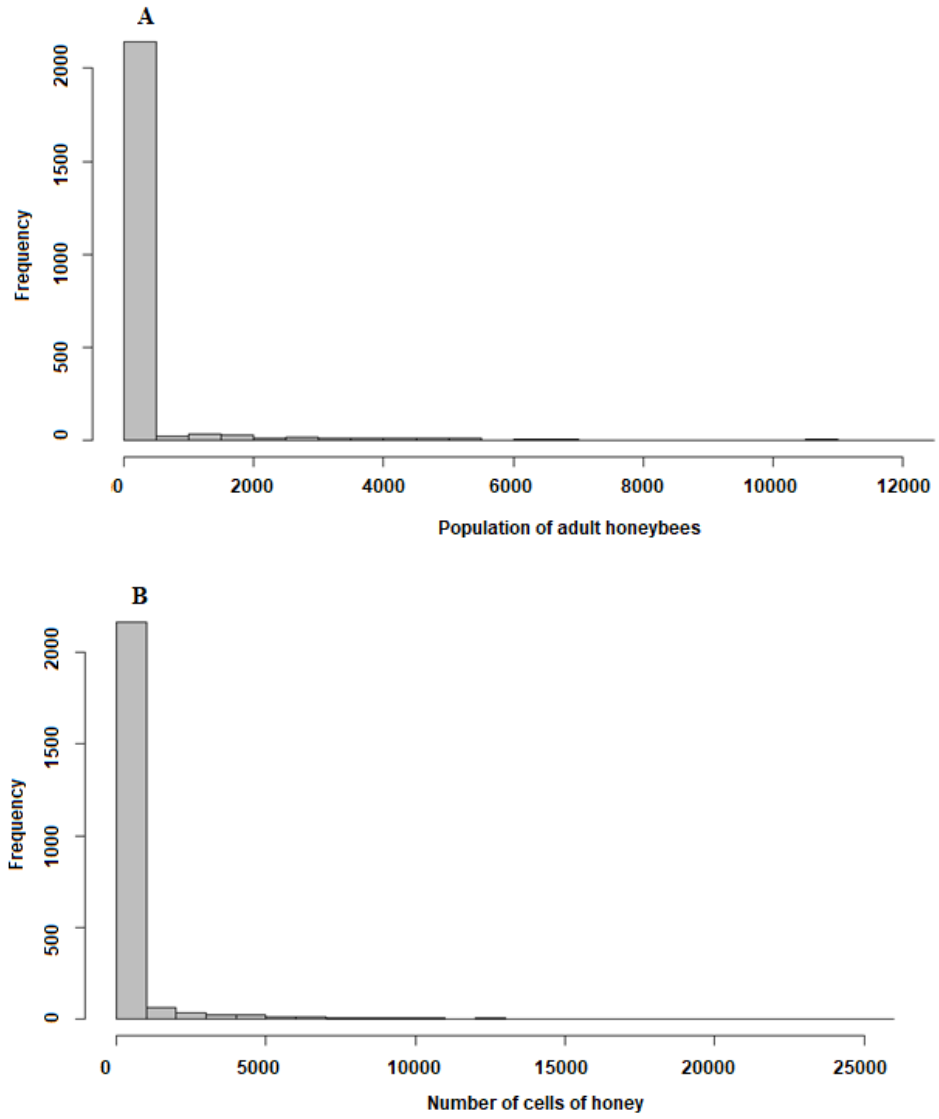

Figure D1: Histograms for samples of adult honeybee populations and number of cells of honey show high number of zeros.

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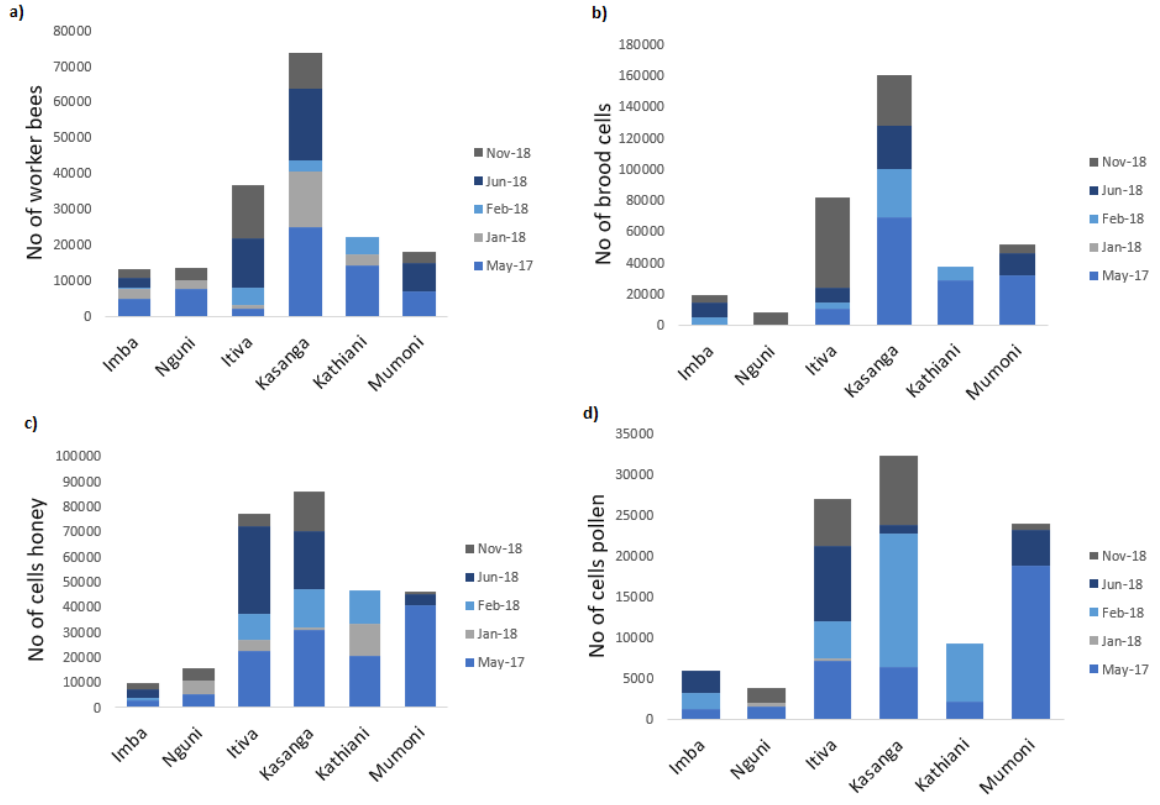

Figure D2: Total honeybee colony strength characteristics in the six sites in the Mwingi study region, Kenya estimated using Liebefeld methods: a) worker honeybees population b) total cells brood, c) total cells honey and d) total cells pollen.

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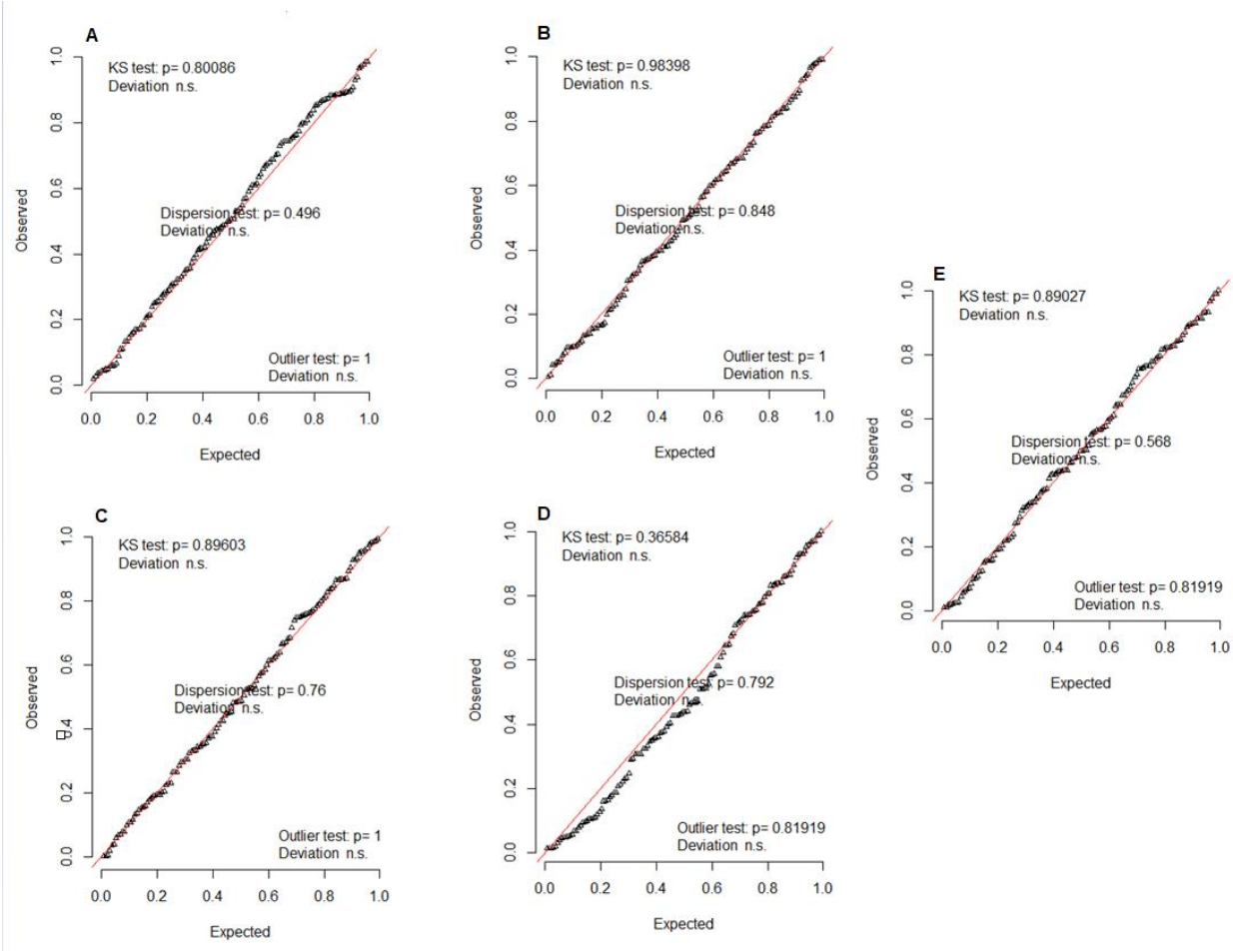

Figure D3: Model residual QQ-plots of observed against expected values at 1km buffer distance for A) population of adult honeybees, B) number of brood cells, C) number of cells of honey, D) numb er of cells of pollen and E) number of cells of eggs.

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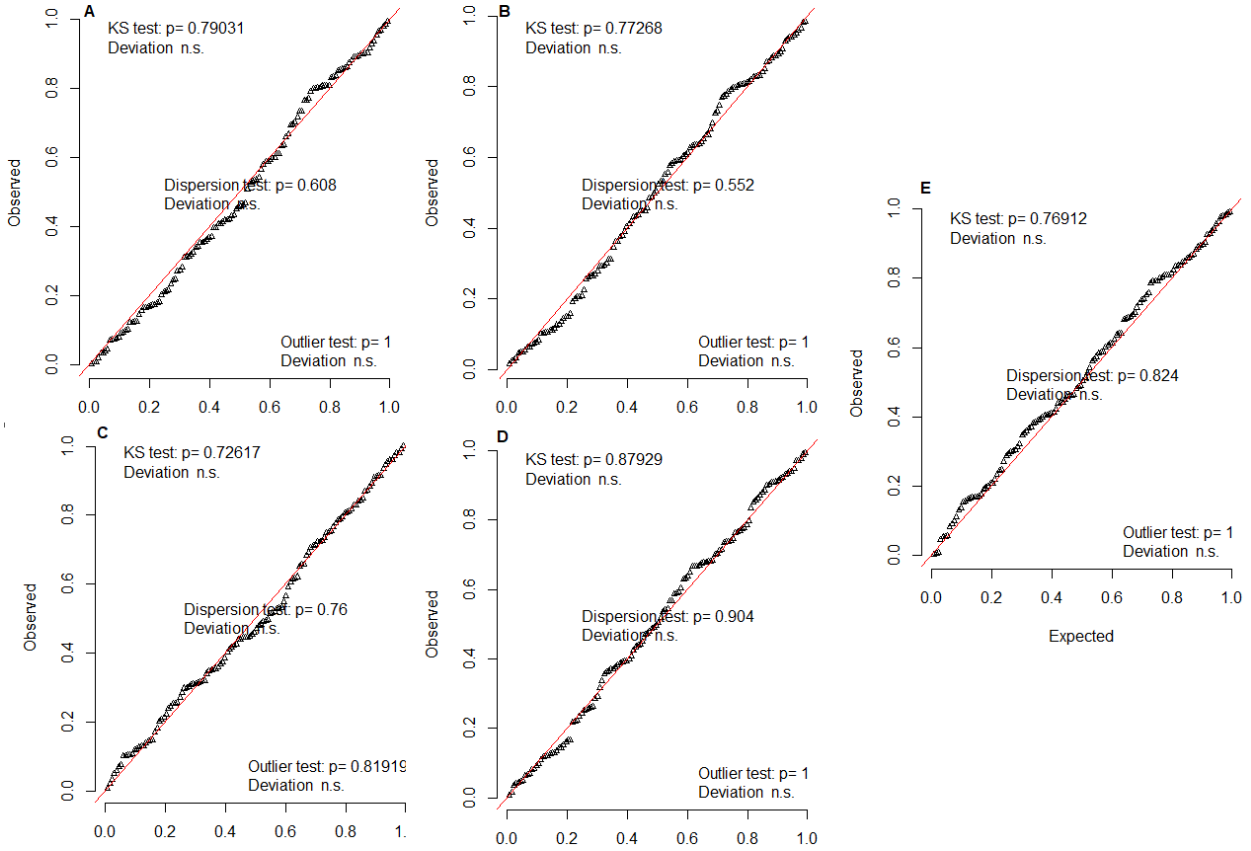

Figure D4: Model residual QQ-plots of observed against expected values at 2.5km buffer distance for A) population of adult honeybees, B) number of brood cells, C) number of cells of honey, D) number of cells of pollen and E) number of cells of eggs.

Table D1: ZINB model parameters of the response of population of adult honeybees (n = 150) to la ndscape fragmentation predictors at 1km and 2.5km radii. Zero component results show how predict ors affect the odds of observing excess zeros in adult honeybee populations while count component results show how predictors affect the population of adult honeybees.

Zero component						**Count component**			
Scale	Variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
1Km	(Intercept)	-77.38	46.47	-1.67	.	61.37	23.12	2.66	*
	FD	48.25	20.99	2.30	*	-22.08	10.09	-2.19	*
	PLC	0.03	0.33	0.10	.	-0.36	0.16	-2.31	*
	LSW	-0.64	0.34	-1.86	.	0.42	0.15	2.76	*
	LPC	0.00	0.03	-0.08	.	-0.02	0.01	-1.69	.
	FNC	0.51	2.77	0.18	.	-3.05	1.35	-2.26	*

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2.5km	(Intercept)	13.56	4.18	3.24	*	4.53	1.64	2.77	*
	PLG	-0.26	0.11	-2.34	*	0.08	0.05	1.66	.
	PLW	-0.15	0.05	-3.09	*	0.04	0.02	2.13	*
	LPH	0.30	0.11	2.63	*	-0.08	0.06	-1.42	.
	PLH	-1.24	0.41	-3.05	*	0.23	0.16	1.43	.

Significance codes: <0.05 '*', > 0.05 '.'; Overdispersion parameter at 1km = 2.11; Overdispersion parameter at 2.5km = 2.21

Table D2: ZINB model parameters of the response of number of brood cells (n = 150) to landscape fragmentation predictors at 1km and 2.5km radii. Zero component results show how predictors affect the odds of observing excess zeros in number of brood cells while count component results show how predictors affect the number of brood cells.

Zero component						**Count component**			
Scale	Variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
1Km	(Intercept)	0.56	0.88	0.64	.	9.27	0.60	15.38	*
	PLC	0.00	0.02	-0.08	.	-0.01	0.02	-0.59	.
2.5km	(Intercept)	18.92	4.80	3.94	*	2.73	2.70	1.01	.
	PLG	-0.34	0.12	-2.90	*	0.18	0.06	2.86	*
	PLW	-0.21	0.05	-3.76	*	0.07	0.03	2.36	*
	LPH	0.49	0.16	2.95	*	-0.05	0.10	-0.54	.
	PLH	-1.66	0.48	-3.49	*	0.27	0.27	1.01	.

Significance codes: <0.05 '*', > 0.05 '.'; Overdispersion parameter at 1km = 2.12; Overdispersion parameter at 2.5km = 2.21

Table D3: ZINB model parameters of the response of number of honey cells (n = 150) to landscape fragmentation predictors at 1km and 2.5km radii. Zero component results show how predictors affect the odds of observing excess zeros in number of honey cells while count component results show how predictors affect the number of honey cells.

Zero component					**Count component**		
Scale	Variable	Estimate	Standard error	z-value	Estimate	Standard error	z-value

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1Km	(Intercept)	-78.64	43.34	-1.81	.	32.50	16.63	1.95	.
	FD	48.70	20.09	2.42	*	-9.26	7.44	-1.25	.
	PLC	0.04	0.30	0.13	.	-0.21	0.12	-1.65	.
	LSW	-0.65	0.33	-1.93	.	0.27	0.13	2.11	*
	FNC	0.60	2.52	0.24	.	-1.66	1.05	-1.57	.
2.5km	(Intercept)	14.31	4.23	3.38	*	3.41	2.47	1.38	.
	PLG	-0.26	0.11	-2.34	*	0.09	0.08	1.22	.
	PLW	-0.16	0.05	-3.26	*	0.06	0.03	2.29	*
	LPH	0.21	0.12	1.80	.	-0.07	0.09	-0.75	.
	PLH	-1.22	0.41	-2.95	*	0.35	0.24	1.49	.

Table D4: ZINB model parameters of the response of number of pollen cells (n = 150) to landscape fragmentation predictors at 1km and 2.5km radii. Zero component results show how predictors affect the odds of observing excess zeros in number of pollen cells while count component results show how predictors affect the number of pollen cells.

Zero component						**Count component**			
Scale	Variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
1Km	(Intercept)	-66.46	42.29	-1.57	.	33.55	24.58	1.37	.
	FD	44.67	18.94	2.36	*	-13.14	10.64	-1.24	.
	PLC	-0.05	0.31	-0.17	.	-0.12	0.20	-0.63	.
	LSW	-0.53	0.32	-1.63	.	0.32	0.19	1.68	.
	FNC	-0.32	2.64	-0.12	.	-0.67	1.66	-0.40	.
2.5km	(Intercept)	12.86	4.01	3.20	*	0.84	2.44	0.34	.
	PLG	-0.23	0.12	-1.86	.	0.15	0.08	1.79	.
	PLW	-0.13	0.05	-2.90	*	0.09	0.03	3.19	*
	LPH	0.16	0.13	1.25	.	-0.15	0.08	-1.76	.
	PLH	-1.03	0.38	-2.69	*	0.48	0.22	2.14	*

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Significance codes: <0.05 '*', > 0.05 '.'; ZI = Zero inflated negative binomial; Overdispersion parameter at 1km = 1.53; Overdispersion parameter at 2.5km = 1.65

Table D5: ZINB model parameters of the response of number of cells of eggs (n = 150) to landscape fragmentation predictors at 1km and 2.5km radii. Zero component results show how predictors affect the odds of observing excess zeros in number of cells of eggs while count component results show how predictors affect the number of cells of eggs.

Zero component						**Count component**			
Scale	Variable	Estimate	Standard error	z-value		Estimate	Standard error	z-value	
1Km	(Intercept)	-58.89	20.38	-2.89	*	-4.49	10.52	-0.43	.
	FD	36.95	12.63	2.93	*	7.21	6.53	1.11	.
2.5km	(Intercept)	18.82	5.96	3.16	*	2.67	3.19	0.84	*
	PLG	-0.27	0.13	-2.12	*	0.07	0.06	1.05	.
	PLW	-0.20	0.07	-2.96	*	0.05	0.04	1.41	.
	LPH	0.57	0.22	2.64	*	-0.21	0.12	-1.78	.
	PLH	-1.83	0.60	-3.04	*	0.46	0.32	1.43	.

Significance codes: <0.05 '*', > 0.05 '.'; Overdispersion parameter at 1km = 2.84; Overdispersion parameter at 2.5km = 3.01

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APPENDIX E: CHAPTER 4 SUPPLEMENTARY TABLES AND FIGURES

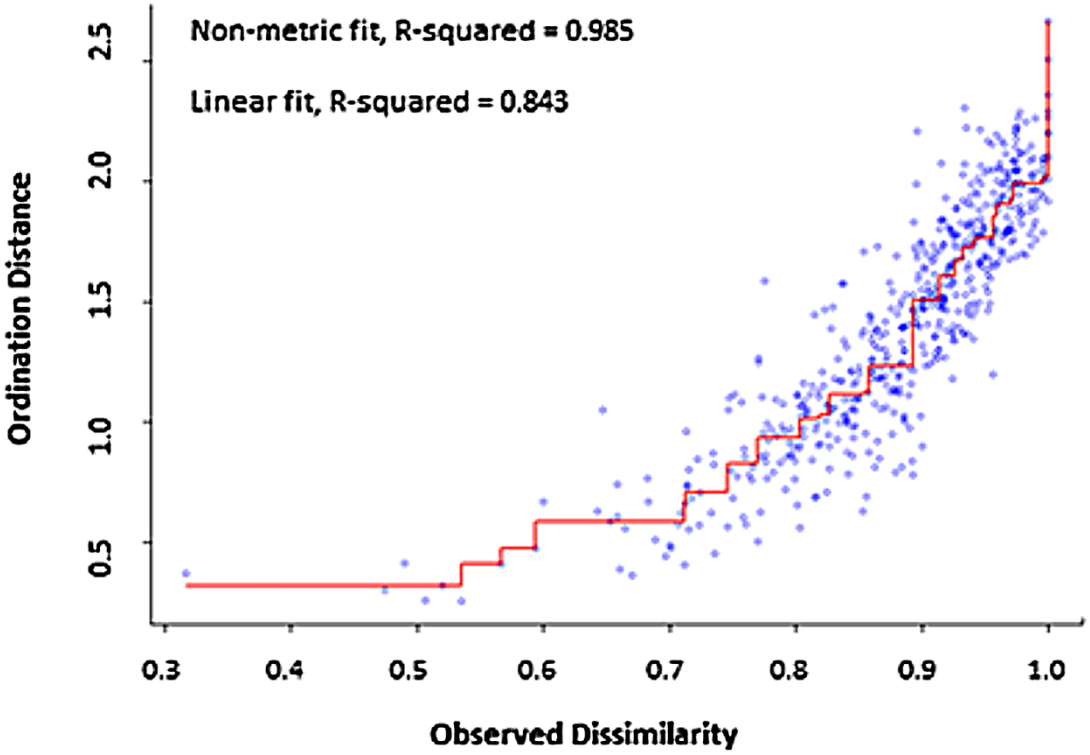

Figure E1: Shepherd's diagram, with correlation statistics demonstrating the goodness of fit of the pollen samples from the NMDS analysis

Pairwise SIMPER with Bray-Curtis similarity test results for the four most separated pairs of sites as derived from the NMDS ordination graph. a) Imba versus Kathiani b) Itiva versus Nguni c) Imba versus Kasanga and d) Imba versus Nguni (Plant species which are primarily responsible for the perceived difference between the sites (up to approximately 50% contribution) are shown in the graphs.

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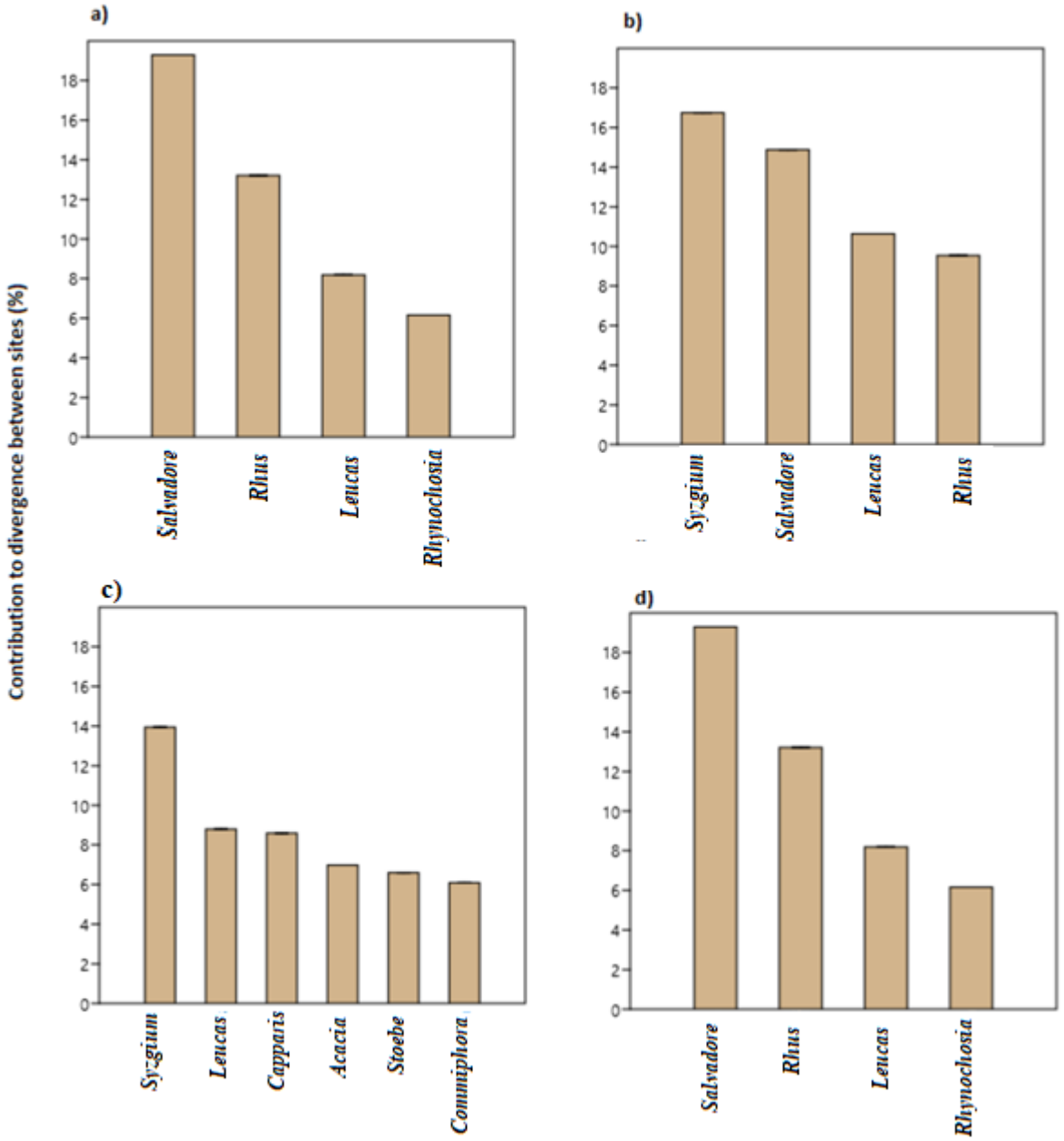

Figure E2: Pairwise SIMPER with Bray-Curtis similarity test results for the four most separated pairs of sites as derived from the NMDS ordination graph. a) Imba versus Kathiani b) Itiva versus Nguni c) Imba versus Kasanga and d) Imba versus Nguni (Plant species which are primarily responsible for the perceived difference between the sites (up to approximately 50% contribution) are shown in the graphs.

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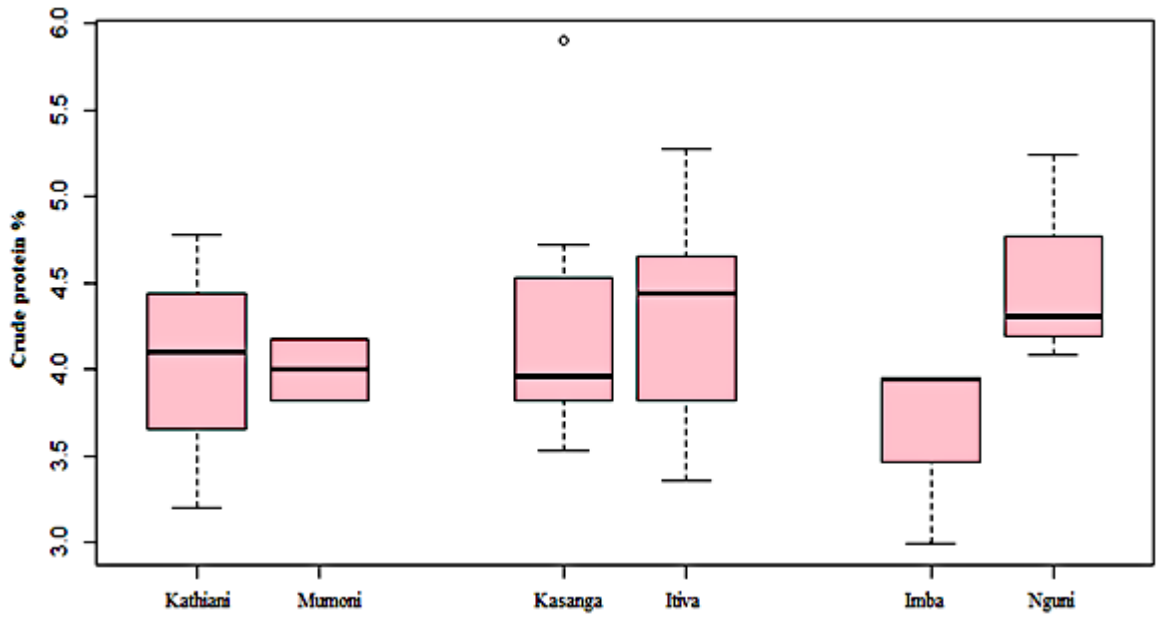

Figure E3: Total crude protein concentration (%) across the six study sites, grouped from left to right as: least degraded, moderately degraded, and highly degraded

Table E1: RAD models, their formulae and use. The formulae in each RAD model shows how the abundance of species at rank r (a_r) is calculated. Descriptions are derived from Gardener (2014)

RAD model	**Formulae**	**Use**
Broken Stick Model	$a_r = J/S\ \Sigma(1/x)$	*J* is the number of individuals, and *S* is the number of species in the community
Lognormal model	$a_r = \exp(\log(\mu) + \log(\sigma) \times N)$	*N* is the normal deviate and μ and σ are the mean and standard deviation of the distribution
Mandelbrot model	$a_r = Jc\ (r + \beta)\ \gamma$	*J* is the number of individuals, γ is a decay coefficient. The addition of the β parameter leads to the P_1 part of the Zipf model becoming a scaling constant, *c*.
Preemption model	$a_r = J\alpha\ (1 - \alpha)\ (r - 1)$ In	*J* is the number of individuals and the

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		parameter α is a decay rate of abundance with rank.
Zipf model	$a_r = J \times P_1 \times r\gamma$	*J* is the number of individuals, P_1 is the proportion of the most abundant species and γ is a decay coefficient

Table E2: Table showing AIC values and matching model names for each study site following the radfit() function in vegan package.

	Kathiani	Mumoni	Kasanga	Itiva	Imba	Nguni
Null	1790.22	1728.98	4902.03	8445.82	1518.54	1939.6
Preemption	608.9	1223.05	891.75	2066.45	360.01	261.96
Lognormal	373.24	389.74	1246.64	1672.69	255.39	464.33
Zipf	667.63	298.44	2334.03	2877.14	346.76	713.07
Mandelbrot	330.57	300.44	564.06	694.12	176.2	265.96

Table E3: Pairwise comparisons (p-values) of Renyi diversities carried out using the Wilcoxon Rank Sum Test

	Imba	**Itiva**	**Kasanga**	**Kathiani**	**Mumoni**	**Nguni**
Imba	1	0.01*	0.02*	0.08^{NS}	0.32^{NS}	0.32^{NS}
Itiva	0.01*	1	0.71^{NS}	0.32^{NS}	0.02*	0.03*
Kasanga	0.02*	0.71^{NS}	1	0.44^{NS}	0.03*	0.05^{NS}
Kathiani	0.08^{NS}	0.32^{NS}	0.44^{NS}	1	0.05^{NS}	0.11^{NS}
Mumoni	0.32^{NS}	0.02*	0.03*	0.05^{NS}	1	0.27^{NS}
Nguni	0.32^{NS}	0.03*	0.05^{NS}	0.11^{NS}	0.27^{NS}	1

Significance codes: ≤ 0.05 '*' ≥ 0.05 '^{NS}';NS = Not significant

Table E4: Pairwise comparisons (p-values) of crude protein concentration (%) across seasons carried out using the Wilcoxon Rank Sum Test

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	May	**January**	**June**	**November**
May	1	0.00*	0.02*	0.15^{NS}
January	0.00*	1	0.87^{NS}	0.15^{NS}
June	0.02*	0.87^{NS}	1	0.24^{NS}
November	0.15^{NS}	0.15^{NS}	0.24^{NS}	1

Significance codes: ≤ 0.05 '*' ≥ 0.05 '^{NS}';NS = Not significant

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APPENDIX F: CHAPTER 5 SUPPLEMENTARY TABLES AND FIGURES

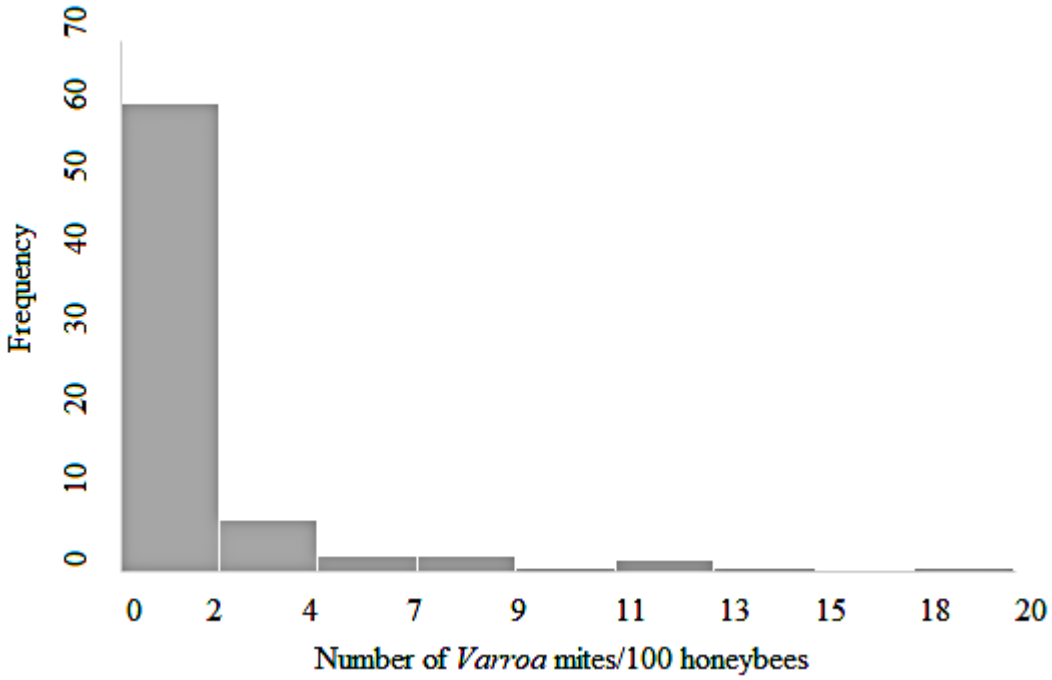

Figure F1: Histogram of number of Varroa mite per a sample of 100 honeybees

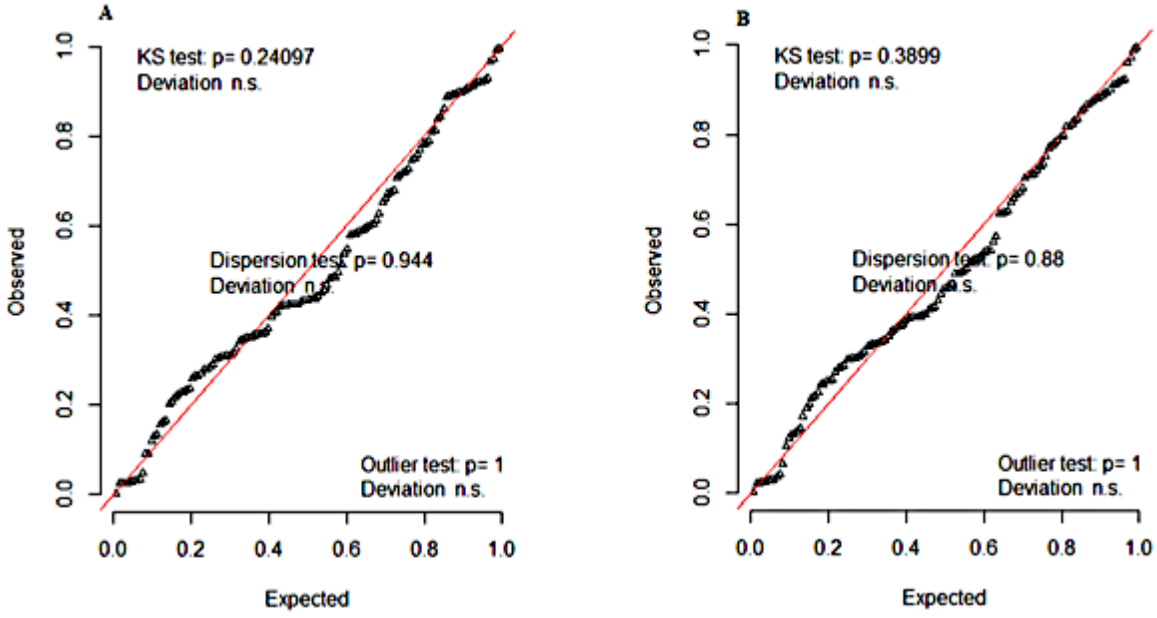

Figure F2: Model residual QQ-plots of observed against expected numbers of Varroa mite against landscape fragmentation variables at A) 1 km buffer scale and B) 2.5 km buffer scale.

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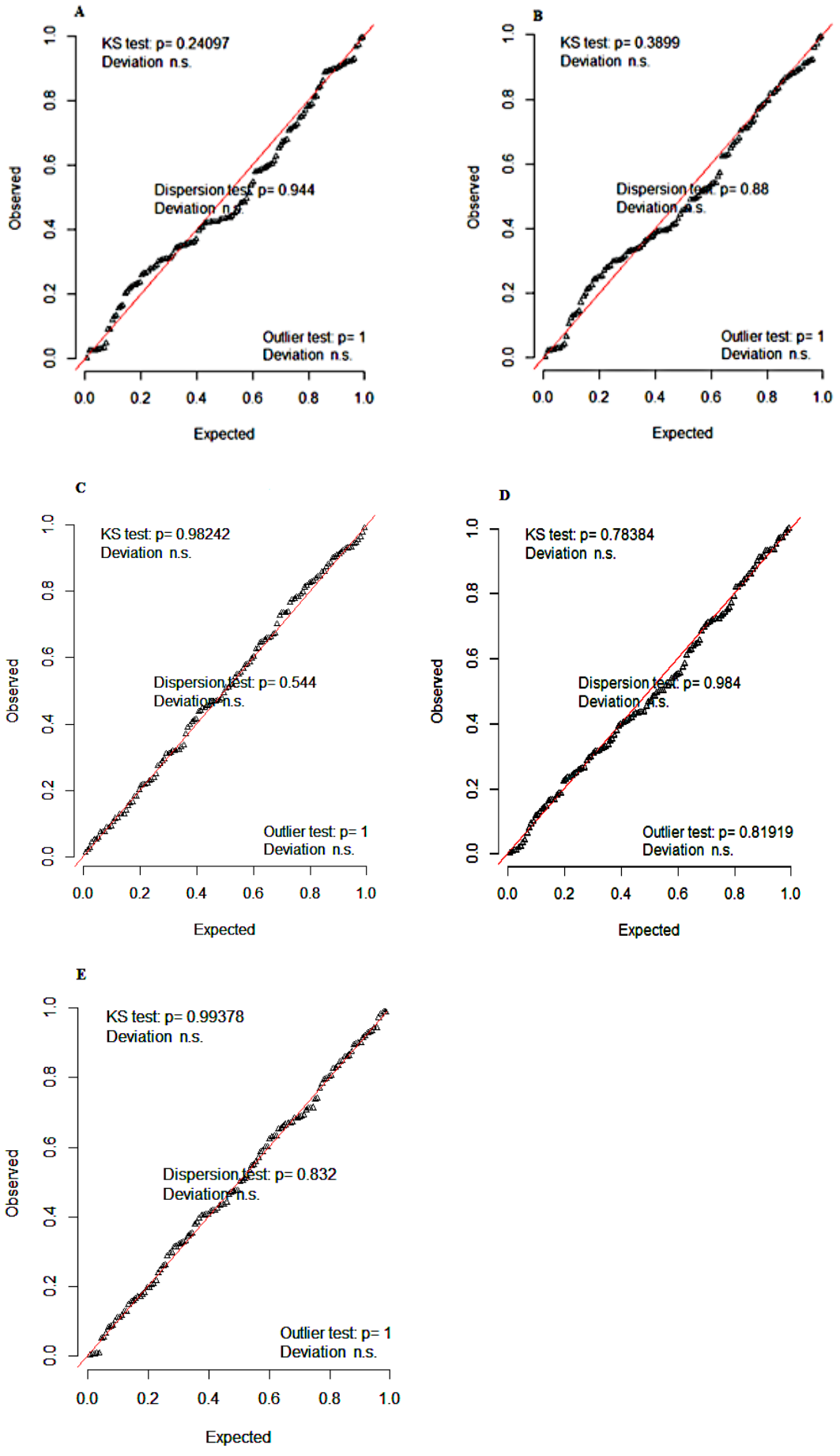

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Figure F3: Model residual QQ-plots of observed against expected values for A) population of adult honeybees, B) number of cells of honey C) number of cells of brood D) number of cells of pollen and E) number of cells of eggs

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APPENDIX G: LANDSCAPE FRAGMENTATION METRICS AT 1KM AND 2.5KM RADIUS

Fragmentation variable	Description	Imba	Mumoni	Itiva	Kathiani	Kasanga	Nguni
PLANDwoody 1km	The proportional abundance of woody vegetation across the landscape at 1 km	10.76	76.972	18.612	41.64	31.132	8.517
PLANDgrass 1km	The proportional abundance of grassland across the landscape at 1 km	16.139	1.577	16.719	9.464	15.723	16.088
PLANDhedges 1km	The proportional abundance of hedges across the landscape at 1 km	3.798	0	11.041	5.047	4.088	6.94
PLANDCropland 1km	The proportional abundance of cropland across the landscape at 1 km	49.367	19.243	45.426	39.432	43.711	46.688
LPIwoody 1km	Largest patch index of woody vegetation at 1 km	5.38	76.972	18.612	36.593	7.233	3.155
LPIgrass 1km	Largest patch index of grassland at 1 km	7.911	0.316	16.719	2.208	1.887	2.524
LPIhedges 1km	Largest patch index of hedges at 1 km	0.633	0	11.041	0.946	1.258	0.946
LPIcropland 1km	Largest patch index of cropland at 1 km	13.924	14.511	45.426	23.659	18.554	0.946
LSIwoody 1km	Largest shape index of woody vegetation at 1 km	3.583	3.594	4.938	2.957	5.5	4.182
LSIgrass 1km	Largest shape index of grassland at 1 km	4.467	2	5.6	4.909	5.467	5.133
LSIhedges 1km	Largest shape index of hedges at 1 km	3.286	0	5.417	3.625	3	3.8
LSIcropland 1km	Largest shape index of cropland at 1 km	5.612	3.25	5.586	5.244	5.471	5.782

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SHDI 1km	Shannon diversity index at 1 km	1.669	0.706	1.751	1.534	1.499	1.815
FD 1km	Fractal dimension index at 1 km	1.602	1.602	1.593	1.612	1.629	1.639
CONTAG 1km	Contagion index at 1 km	16.397	57.091	17.279	32.86	17.979	14.2
SI 1km	Splitting index at 1 km	20.795	1.629	38.487	5.53	10.492	36.475
PLANDwoody 2.5km	The proportional abundance of woody vegetation across the landscape at 1 km	11.426	78.636	13.961	47.347	30.055	6.218
PLANDgrass 2.5km	The proportional abundance of grassland across the landscape at 1 km	17.24	2.98	19.676	8.135	16.786	20.273
PLANDhedges 2.5km	The proportional abundance of hedges across the landscape at 1 km	6.32	0.707	8.801	3.436	4.257	7.027
PLANDCropland 2.5km	The proportional abundance of cropland across the landscape at 1 km	49.596	15.303	49.874	35.776	36.958	45.905
LPIwoody 2.5km	Largest patch index of woody vegetation at 1 km	2.477	76.869	13.961	43.153	14.256	6.218
LPIgrass 2.5km	Largest patch index of grassland at 1 km	1.871	0.253	19.676	0.404	1.059	20.273
LPIhedges 2.5km	Largest patch index of hedges at 1 km	0.455	0.101	8.801	0.152	0.245	7.027
LPIcropland 2.5km	Largest patch index of cropland at 1 km	5.662	10.202	49.874	13.997	4.179	45.905
LSIwoody 2.5km	Largest shape index of woody vegetation at 1 km	8.484	5.342	10.177	3.887	12.256	9.087
LSIgrass 2.5km	Largest shape index of grassland at 1 km	13.514	6.875	15.05	10.654	15.699	13.634

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LSIhedges 2.5km	Largest shape index of hedges at 1 km	9.957	3.5	11.259	7.294	10.658	10.542
LSIcropland 2.5km	Largest shape index of cropland at 1 km	15.22	7.093	14.276	12.042	14.365	14.146
SHDI 2.5km	Shannon diversity index at 1 km	1.729	0.787	1.729	1.476	1.476	1.861
FD 2.5km	Fractal dimension index at 1 km	1.659	1.598	1.659	1.629	1.629	1.669
CONTAG 2.5km	Contagion index at 1 km	18.648	67.089	18.648	38.22	38.22	16.581
SI2.5 km	Splitting index at 1 km	86.859	1.664	86.859	4.805	4.805	71.268